

LIMNOLOGICAL INVESTIGATIONS ON RESPIRATION, ANNUAL
MIGRATORY CYCLE, AND OTHER RELATED PHENOMENA
IN FRESH-WATER PULMONATE SNAILS

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INTRODUCTION

Periodic movements of aquatic organisms induced by seasonal environmental changes, both physical and chemical, have been reported by many investigators. The fresh-water pulmonate gasteropods exhibit these phenomena in a marked way. Accompanying the seasonal migrations from shallow to deep water, or the reverse, are certain alterations in their mode of respiration which are necessary to meet the exigencies of their changed environment. The cause of the annual migratory cycle, the breathing behavior, and other related phenomena constitute the subject matter of this paper.

Nine species of pulmonate snails, representing five genera and three families have been considered. Four of the species, *Lymnaea stagnalis appressa* (Say), *Lymnaea palustris* (Müller), *Lymnaea emarginata angulata* (Sowerby), and *Lymnaea megasoma* Say are members of the family Lymnaeidae. The family Planorbidae is represented by *Helisoma antrosom percarinatum* (Walker), *Helisoma campanulatum smithi* (Baker), and *Helisoma trivolvis* (Say). The remaining two species, *Physa parkeri* Currier, and *Physa sayii crassa* Walker belong to the Physidae.

¹ Contribution from the Department of Zoology, University of Michigan, and from the University of Michigan Biological Station.

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Since a description of the regions in which these studies were made is given elsewhere in this paper, only the general environmental conditions and distribution of the snails are described here.

Lymnaea stagnalis appressa (Say), (fig. 2). Occurs in protected situations, along sandy or mucky shoals in vegetation areas. Baker (1928) lists this subspecies as occurring in North America from about the 37th and 41st parallels of north latitude to the Arctic Ocean.

Lymnaea palustris (Müller), (fig. 4). Inhabits swamps, protected vegetation zones of lakes, slow-moving streams, and stagnant ditches. Frequently found in pools that dry up during the summer. In such a habitat, the molluscan fauna is active for only three or four months during the year. This snail has a rather wide distribution, and occurs in most of the country east of the Rocky Mountains (Baker, 1928).

Lymnaea emarginata angulata (Sowerby), (fig. 3). Ordinarily found in exposed littoral regions, clinging tightly to rocks, or buried in the sand or mucky bottom. Occurs from Michigan to Minnesota and south to central Wisconsin (Baker, 1928).

Lymnaea megasoma Say, (fig. 1). Inhabits swampy regions of protected bays or rivers. Occurs from northern New England (Vermont), west to Minnesota, Iowa and Manitoba; and from northern Ohio northward to about latitude 57° N. in British America (Baker, 1928).

Helisoma antrosom percarinatum (Walker), (fig. 9). Occurs widely in lakes. Found in sheltered vegetation zones and in exposed littoral regions. Distribution confined to the Great Lakes region (Baker, 1928).

Helisoma campanulatum smithi (Baker), (fig. 8). Commonly found in exposed areas of the lake; frequently in sheltered situations. Apparently confined to Douglas Lake, Cheboygan County, Michigan (Baker, 1928).

Helisoma trivolvis (Say), (fig. 7). In quiet, more or less stagnant water. Occurs from the Atlantic Coast and Mississippi River drainage northward to Arctic British America, Alaska, and southward to Tennessee and Missouri (Baker, 1928).

Physa parkeri Currier, (fig. 5). Inhabits sheltered bays or open and exposed areas of lakes. Found in several lakes of northern Michigan (Goodrich, 1932).

Physa sayii crassa Walker, (fig. 6). Occurs in most exposed areas of lakes. Restricted in its distribution to Michigan and Wisconsin (Baker, 1928).

Field observations and experimental work were begun in the summer of 1926, and continued during the summers of 1928 and 1930. In the early fall of 1931, work was resumed and was in continuous progress until the spring of 1933.

That air-breathing snails inhabit the deeper regions of fresh-water lakes was first pointed out by Forel (1869). Since that time, many other records

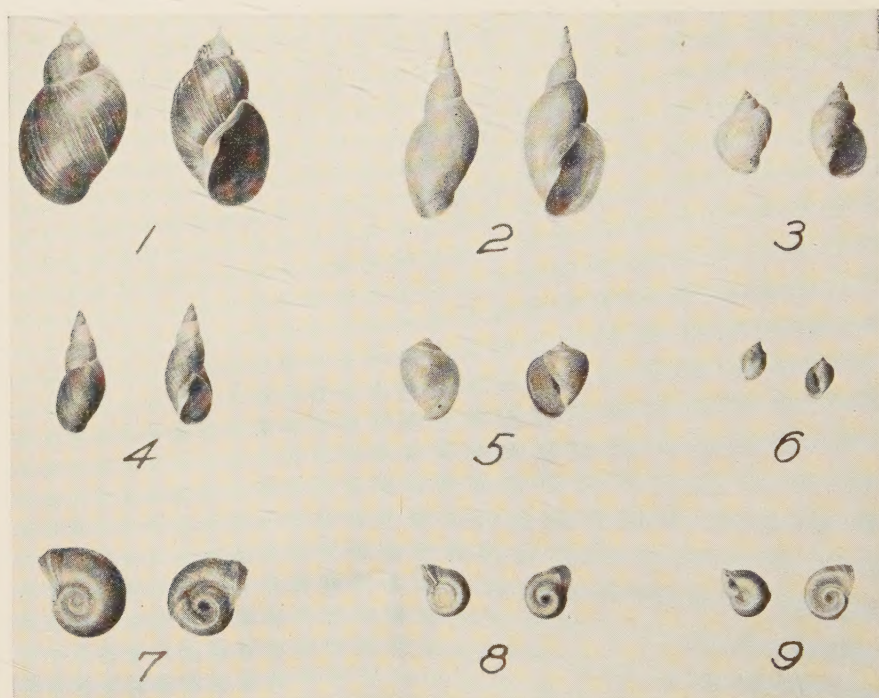


PLATE XXXVIII

- FIG. 1. *Lymnaea megasoma*
 FIG. 2. *Lymnaea stagnalis appressa*
 FIG. 3. *Lymnaea emarginata angulata*
 FIG. 4. *Lymnaea palustris*
 FIG. 5. *Physa parkeri*
 FIG. 6. *Physa sayii crassa*
 FIG. 7. *Helisoma trivolvis*
 FIG. 8. *Helisoma campanulatum smithi*
 FIG. 9. *Helisoma antrosum percarinatum*

of pulmonate snails dredged from deep water of inland lakes have appeared. Pauly was one of the first to demonstrate that lymnaeid snails possess a cutaneous respiration sufficiently active to supplant the pulmonary respiration. His observations were based on one specimen of *Lymnaea stagnalis* that lived for ninety days in an aquarium without access to the atmosphere. During this time, not a drop of water entered the pulmonary sac. Evidently, cutaneous respiration is sufficient to maintain life. Clessin (1877) advanced the theory that lymnaeid snails normally

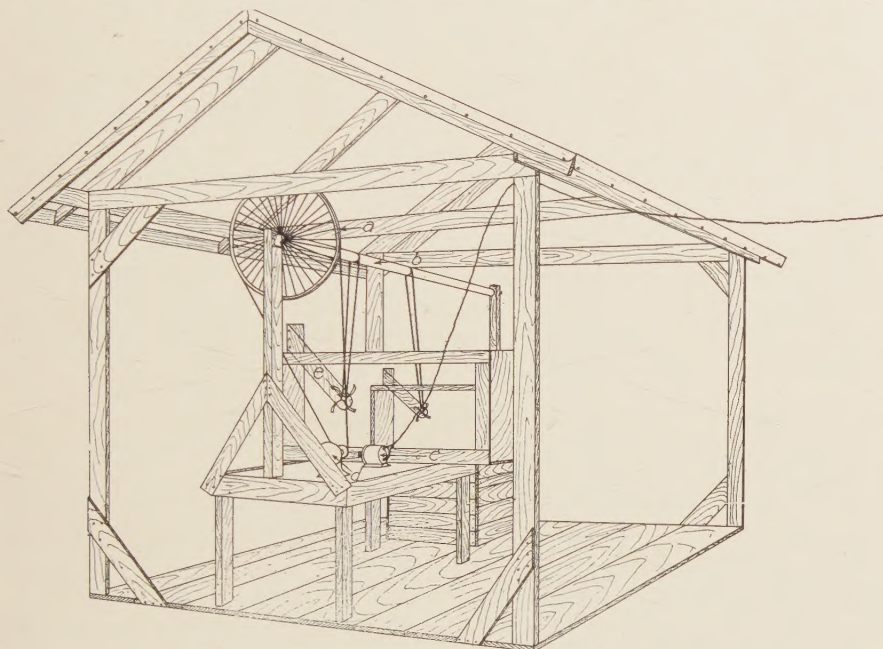


FIG. 10. Apparatus for aeration of water

- | | |
|------------------|-------------------|
| a. Bicycle wheel | d. Reducing gears |
| b. Countershaft | e. Water wheel |
| c. Motor | |

utilize the dissolved oxygen of the water and come to the surface only when compelled to do so by an unusually high temperature. Willem (1896) expressed the opinion that in the suborder Basommatophora cutaneous respiration is more important than pulmonary respiration, but it alone is not sufficient to maintain life. Walter (1906) stated that breathing without coming to the surface may, in the case of pulmonates, be considered as abnormal. Observations by Moquin-Tandon (1855), Saint-Simon (1853), Pauly (1877), and Walter tend to demonstrate that *Lymnaea* is unable to adapt itself suddenly to the water-breathing habit. Roszkowski (1914) called attention to the singular fact that the lung of profundal lymnaeids

in Lake Geneva is always filled with water, apparently functioning as a gill. He also expressed the belief, unsubstantiated by experimental work, that an increase in the temperature of the water is accompanied by a corresponding increase in oxygen consumption by the animal.

As indicated in the major contributions cited, practically all of the observations and experimental work have been based on lymnaeid snails. It is clearly evident that opinions vary as to the method employed by pulmonate snails in securing oxygen under different environmental conditions. The circumstances that bring about respiration, cutaneous or pulmonary, were not discussed, and, if mentioned, were not verified by experimental evidence. To the writer's knowledge, no contributions have been made that offer an explanation for the causes of the periodic migratory cycle of lake pulmonates.

Most of the field and experimental work was done in the environs of the University of Michigan Biological Station, Douglas Lake, Cheboygan County, Michigan. Field observations during the autumn, winter, and spring months of 1932 and of 1933, were made on several lakes and streams in the vicinity of Ann Arbor, Michigan. In addition to the regions mentioned, field data were obtained from many other lakes and streams in both the lower and upper peninsulas of Michigan.

ACKNOWLEDGMENTS

The author is especially indebted to Professor Paul S. Welch under whose direction this work was conducted. Acknowledgments are due also to Professor George R. LaRue for the use of facilities at the University of Michigan Biological Station; to Mr. Calvin Goodrich, of the University of Michigan Museum of Zoology, for the identification of snails; to Mr. William M. Clay for photographs; and to Mr. E. L. Cheatum for making the drawings shown in plate XXXIX.

EQUIPMENT AND METHODS

Observations on submerged snails in their natural habitats were made in water 2-9 meters deep by the use of a diving helmet. Temperatures were determined with Tycos maximum-minimum thermometers. Chainomatic analytical balances were used for weighing snails. A refrigeration room which maintained a constant temperature of 5.5°C. was available when low temperatures were desired.

In the field dissolved oxygen was determined by the Rideal-Stewart modification of the Winkler method (Am. Publ. H. Assoc. 1925). Samples collected in the field were treated at once with the reagents up to the final titration point. If return to the laboratory occurred within a period of five hours after the samples were taken, final titration was done there; if not, analyses were completed in the field. For the determination of oxygen con-

tent in small amounts of water, Lund's Micro-Winkler method (1921) was used. This method was of distinct advantage in shortening the duration of tests, thus making it possible to follow the course of respiratory exchanges over relatively short periods.

In order to keep large quantities of snails in stock for laboratory work, it was necessary to devise a method which would reduce to the minimum mortality due to adverse conditions in captivity and insure healthy individuals for experimental work. The following method proved very satisfactory. Snails were reared in glass aquaria varying in capacity from 9 to 420 liters. A layer of sand and gravel about $2\frac{1}{2}$ centimeters in thickness was placed in the bottom of each aquarium. This served as a support for the roots of aquatic plants which were grown as a source of food supply, as well as for oxygenation of the water. Ordinarily, as long as the aquaria were not overcrowded with snails, the water remained clear due to a well balanced condition between plant and animal life. However, when conditions adverse to snail growth developed, the water was siphoned out and fresh lake water substituted. Filamentous algae and *Elodea* are excellent aquarium plants for snail propagation. They are very active in photosynthesis, and are utilized as food by the snails. In addition to aquarium-grown foods, lettuce leaves and thin slices of apple were fed to the snails two or three times a week.

In the early part of this work, it was discovered that conditions favorable for one species of snail may be rather adverse for another. The depth of water in aquaria in which snails were reared proved to be a very important factor. The two marsh-inhabiting species, *Lymnaea megasoma* and *Lymnaea palustris*, thrived best in aquaria containing 7 or 10 centimeters of water, whereas mortality among these snails was always high in aquaria with 25 and 30 centimeters of water. With the exception of difference in depth, other conditions, such as plant life, food, and temperature, were the same. The other species, which were all lake-inhabiting animals, lived equally well in either deep or shallow water. An explanation for this behavior can only be postulated. The species mentioned above are invariably found, during the summer months, in water 7-10 centimeters deep or on the surface, and transference from such a habitat into deeper water may retard, or in some cases prevent, their movement to the surface. Whether pressure, internal causes, or other factors play an important role in this behavior is not known.

A series of water wheels provided with paddles (fig. 10) was used for aeration in the larger aquaria. By cupping the paddles and submerging the wheels to their axles, sufficient air was introduced when the wheels were in motion to maintain an oxygen content closely approximating surface lake water. To each wheel (e), was attached a pulley turned by a belt which was connected directly to an overhead counter-shaft (b). This counter-shaft

was 10 centimeters in diameter, 2.5 meters long and supported at either end by a babbit bearing. By means of a bicycle wheel (a) attached to one end of the shaft, and a series of gears (d) between the wheel and the motor (c), the speed was reduced so that the water wheels provided ample aeration without excessive agitation. Power was furnished by a one-half H. P. electric motor. In the laboratory at Ann Arbor, water in which snails were reared was aerated by passing through it a stream of compressed air.

RESPIRATION

Pulmonary Sac

Alteration in shape of the pulmonary sac occurs mainly at the anterior end of the chamber and during the respiratory act. This change occurs when the breathing pore is brought into position at the surface of the water and withdrawn after air has been taken into the chamber. In the Lymnaeidae and Physidae, the anterior end of this sac is frequently drawn out siphon-like. The length and general shape of this tube-like portion depends on the animal's proximity to the surface film. The larger members of the families mentioned have been seen to produce a siphon-like tube at least 7 millimeters in length in order to reach the surface of the water. *Helisoma triivolvis* has also been observed, although infrequently, to extend the end of its pulmonary sac in tubular fashion beyond the rim of the shell. However, this species is the only one of the three belonging to the genus *Helisoma* in which this alteration has been seen. Ordinarily, when in breathing position, the anterior end of the sac is dome-shaped in the Lymnaeidae and Physidae (figs. 11-16). In the genus *Helisoma* (figs. 17-19), this dome-shaped condition is not easily discernible since the respiratory orifice is very seldom projected beyond the peristome of the shell.

The pulmonary sac in *Physa* and *Helisoma* lies on the left side of the body, whereas, in *Lymnaea*, it is located on the right (figs. 11-19). Although the general position of the major part of the pulmonary sac does not vary within a genus, the pulmonary opening varies considerably, depending on the general movements and body position of the animal when breathing. When the foot of *Lymnaea* is completely extended on the surface film, the respiratory opening is usually located just within the peristome and opposite the parietal wall (figs. 11-14). In *Physa* (figs. 15-16), it is situated within the peristome but almost directly opposite the upper part of the columella. In *Helisoma*, due to the flattened shape of the shell, the respiratory pore (figs. 17-19) is situated within the peristome, above and to the left of the snail's head. In this genus, however, the opening of the pulmonary sac has been observed to be shifted so that it lies directly over the center of the head.

The capacity of the pulmonary chamber varies not only intraspecifically with the size of the snail but also in different genera having approxi-

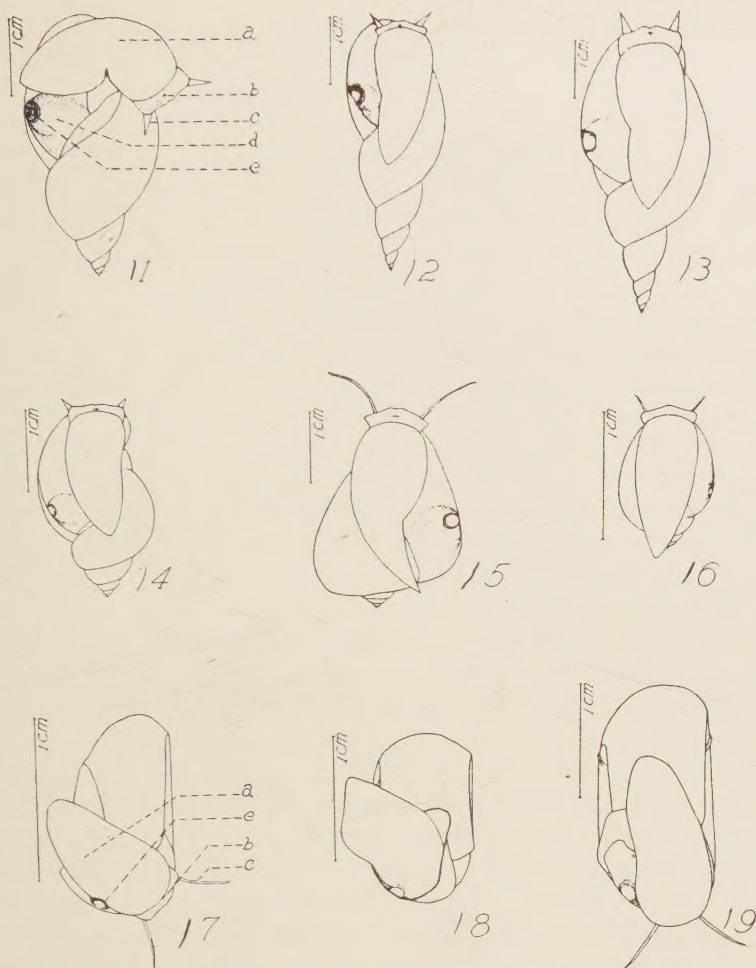


PLATE XXXIX

Snails showing pulmonary sacs in breathing position

- a. Foot-like body
- b. Mouth
- c. Tentacle
- d. Pulmonary sac
- e. Pulmonary opening

FIG. 11. *Lymnaea megasoma*

FIG. 12. *Lymnaea palustris*

FIG. 13. *Lymnaea stagnalis appressa*

FIG. 14. *Lymnaea emarginata angulata*

FIG. 15. *Physa parkeri*

FIG. 16. *Physa sayii crassa*

FIG. 17. *Helisoma antrosum percarinatum*

FIG. 18. *Helisoma campanulatum smithi*

FIG. 19. *Helisoma trivolvis*

mately the same amount of body tissue per gram weight. This conclusion was arrived at by measuring the capacities of pulmonary chambers by keeping count of the air bubbles released in artificial deflation. By careful manipulation, air bubbles may be forced from pulmonary sacs regardless of the size of the snail. Since it was necessary not only in this experiment but in later experiments to control the size of the air bubbles emitted, a special method had to be devised. Air bubbles released in deflation tend to vary in size in proportion to the size of the pulmonary aperture. Large apertures release large air bubbles, and vice versa. However, by careful adjustment of the pressure applied to the pulmonary sac of different species, the emission of uniform air bubbles was made possible. Thus by the application of a small pressure on a large pulmonary sac with a large aperture, the air bubbles discharged were of approximately the same size as those released by a small pulmonary sac upon the application of greater pressure. The increased thickness of the pulmonary walls of a large snail compared to those of a smaller snail would appear to require greater pressure for deflation regardless of the aperture size. However, the deflations of hundreds of snails tend to demonstrate that a large snail is more sensitive to the release of air bubbles than a smaller one.

Table 1 shows the average number of air bubbles released by thirty snails of each species. All snails were of approximately uniform size and collected at random from the rearing aquaria. All had had an equal op-

TABLE 1
AVERAGE NUMBER OF AIR BUBBLES RELEASED BY 30 SNAILS OF EACH SPECIES

Species	Avg. ht. or diam. of shells in mm.	Avg. wt. in gm. body tissue	Avg. no. air bubbles released
<i>L. emarginata angulata</i> ...	20 (ht.)	0.87	12
<i>L. palustris</i>	28 (ht.)	0.70	15
<i>L. stagnalis appressa</i>	45 (ht.)	3.60	22
<i>P. sayii crassa</i>	10 (ht.)	0.15	5
<i>P. parkeri</i>	17 (ht.)	0.70	16
<i>H. antrosom percarinatum</i>	16 (diam.)	0.38	7
<i>H. campanulatum smithi</i> ..	16 (diam.)	0.43	9
<i>H. trivolvis</i>	22 (diam.)	0.58	14
<i>L. megasoma</i>	38 (ht.)	3.50	28

portunity of reaching the surface for air and as a consequence their pulmonary sacs were inflated to an average distension under normal aquarium conditions. One can readily see that there appears to be a definite correlation between the capacity of the pulmonary sac and the weight of the snail. However, this relationship between volume and weight is not in direct proportion. The capacity of the pulmonary sacs in the smaller snails is much greater in proportion to their weight than it is in the larger ones.

BREATHING BEHAVIOR

Ascent to surface.—Aquatic plants, rocks, and organic debris all serve as substrata over which snails may travel in making their way to the surface of the water. The animals, while traveling over these structures by gliding or hunching movements (Walter, 1906), lay down their own highway in the form of a mucous path. Ascent to the surface by utilization of various objects in the water is by far the most common method employed in vegetation areas.

In regions where the water is quiet, snails may construct their own paths in the form of slime strands, which are laid down web-like, the ends of the strands being supported by objects in the water. The ability of snails to produce and utilize such paths is well exemplified in the large marsh snail *L. megasoma*. Usually within one or two days after several of these animals have been placed in an aquarium, they have laid down so many slime strands that innumerable paths extend from objects on the surface of the water to the sides, ends, and bottom of the aquarium. The snails then glide over these highways, feeding as they go on the vegetation that has become entangled in the slime, ultimately reaching the surface. *H. trivolvis* and *L. emarginata angulata*, when placed in an aquarium in which these strands had been produced by other species, were observed to utilize them as paths for their own ascent. Slime threads have an unusual tensile strength. Three large *L. megasoma* were seen to use the same mucous thread simultaneously in ascending to the surface, following each other in single file. When such a weight is placed on one strand, it becomes stretched but immediately returns to the original position when the weight is removed. The Lymnaeidae and Physidae produce and utilize these structures much more frequently than the Planorbidae. The smaller *Physa* often secrete strands invisible to the naked eye. A snail travelling over such a strand appears to be merely suspended in the water and only by passing a pencil or other object around the snail, thus breaking its support, does one become aware of this thread.

Besides utilizing objects in the water for reaching the surface, the ascent may be accomplished by the ability of the snail to suddenly rise from the bottom of the aquarium or lake to the surface, floating up like a cork held under water and suddenly released. This feat cannot be accomplished, however, unless the snail has previously been to the surface and consequently has air in its pulmonary sac. Snails have also been observed to suddenly release their hold on the surface film and drop to the bottom of the aquarium. Walter has observed *Lymnaea palustris* ("*L. elodes*") suspended in the middle of an aquarium by an invisible mucous thread attached to an object on the surface or floor of the aquarium. A snail, if anchored to the bottom, may "gradually spin its way to the surface," or "climb down such an anchorage." He explains that this behavior is made possible by the al-

teration of the animal's specific gravity, due either to the addition of air bubbles or deflation of the lung. Obviously, the specific gravity of the animal must be changed in order to make possible the sudden rise from the floor of the aquarium to the surface or the reverse.

The mechanics involved in changing the specific gravity of the animal can only be postulated. That air in the pulmonary sac is necessary for flotation has been mentioned previously; it is assumed, then, that a snail having sufficient air in the sac to sustain its weight at the surface can, by contraction of the pulmonary sac, reduce the volume of air, thus enabling the animal to sink. Upon dropping to the bottom of the aquarium, it can, by relaxing the muscles of the mantle wall, bring about a sufficient increase in the volume of air within the sac to enable it to float to the surface. Such an activity would make it possible for any snail with sufficient air in the pulmonary sac to return to the surface in the manner described. This behavior has been observed many times in the Lymnaeidae, Physidae and, in a few instances, in *H. trivolvis*.

The apparent inability of some snails to regain the surface by flotation, after having descended to the floor of the aquarium by rapid sinking unaccompanied by the release of visible air bubbles, may be explained as follows: While the snail is on the surface, air is expelled so gradually from the lung cavity that tiny bubbles thus made are invisible to the naked eye. The larger snails, such as *L. megasoma* and *L. stagnalis appressa*, cannot be supported by the surface film alone and, consequently, air in the pulmonary sac must supply most of the necessary buoyancy for supporting these animals upon the surface. After a gradual and very slow elimination of air from the lung, the buoyancy of this organ is reduced to such an extent that it alone cannot support the weight of the snail without the aid of the surface film. As soon as the surface film is broken by contraction of the foot, the animal sinks to the bottom. Snails descending to the aquarium floor in such a manner would have to resort to methods other than flotation in regaining the surface.

The following observations seem to substantiate these hypotheses. Just as the animal begins its descent after breaking the surface film, the exposed portion of the pulmonary sac has been seen to contract. Observations on the smaller Physidae, which possess shells so thin and transparent that the organs are visible through them, have disclosed the expansion of the pulmonary sac before the snail releases its hold on the floor of the aquarium and floats to the surface. The strength of the mantle muscles that surround the lung cavity can be demonstrated by inserting a wooden probe into the open aperture of a large snail, such as *L. megasoma*. The walls then contract so tightly on the probe that the entire animal can be lifted out of the water, the weight being borne by the muscles of the pulmonary sac. It would mean, from this experiment, that the muscles of the mantle are

powerful enough to reduce the volume of air by compression accomplished by their contraction. Many close observations on snails, before they descend in the manner described, have not revealed the visible discharge of air bubbles from the lungs. However, when snails are placed in hot water or when the pulmonary sac is probed, they will emit a stream of air bubbles and sink to the bottom. Lloyd (1854) discovered that by placing a drop of salt upon the outstretched foot of *Lymnaea*, the animal would discharge air bubbles and sink to the bottom of the aquarium. When such an experiment was repeated several times on the same individual, the animal was so weakened that it had to be taken out of the water to save its life.

In exposed areas of lakes, vegetation is usually rather sparse or may be absent. Snails occurring in such habitats are forced to maintain a rather tenacious hold on any surface over which they are moving in order to prevent being washed shoreward. The use of mucous strands as paths for movement in such regions is impossible. It has been observed that a few snails float to the surface when the water is relatively quiet, but the majority, that emerge for air, use the hunching and gliding methods of locomotion. If plant stalks or other objects, such as rocks, are present and extend above the surface film, the snails may utilize them in reaching the air. In most cases, however, the snails inhabiting such an area migrate shoreward during the summer months. Many of those that emerge for air continue this migration until the water is so shallow that it is possible, by a twisting of the shell and body, to break the surface film with the pulmonary siphon without removing the foot from the substratum.

Movements at surface.—After a snail has reached the surface of the water, its body must be oriented in such a manner as to allow the siphon-like respiratory tube to be projected through the surface film. Such movements are dependent largely on the need of the snail for air. As pointed out by Lloyd (1854), a specimen of *Lymnaea stagnalis*, whose lung chamber has been deflated, will, upon its return to the surface, creep up the side of the aquarium until the foot projects one or perhaps two centimeters above the water line before opening its aperture. In this position, a large portion of the pulmonary sac is exposed. Snails, however, that have easy access to the surface and are not interfered with, orient their bodies in the following manner: since the air chamber in the Lymnaeidae is located on the right side, the animal must swing the body into position with this side uppermost, whereas, in the Physidae, the air chamber is on the left and consequently the swing is in the opposite direction. The Planorbidae, when moving at the surface, ordinarily attach the foot to some solid object rather than expand it on the surface film. This behavior may be influenced by the flattened shape of the shell. In order, then, for *Helisoma* to bring the pulmonary opening into position for breathing, the snail must break the surface film with the shell, thus projecting its rim above the surface of the water. As previ-

ously mentioned, *H. trivolvus* has been seen to extend its pulmonary sac in the form of a siphon through the surface film with the shell still submerged. Such behavior has not been observed in the other two species of Planorbidae.

Walter's description of the breathing of *L. palustris* ("*L. elodes*") serves admirably for the larger Lymnaeidae and for *P. parkeri*; consequently, it is reproduced here in his own words: "Apparently snails are first made aware that the surface has been reached by the aid of their tentacles, for it is not until the tip of the tentacle has touched the surface film that the swing of the body is made which brings the respiratory tube into position for use. The opening of this tube at the surface is ordinarily accompanied by an audible 'smack' which aids the observer materially in determining the precise instant when the respiratory cavity is exposed to the air. After filling the respiratory chamber with air the snail closes and withdraws the tube, and goes on its way." *H. antrosom percarinatum*, *H. campanulatum smithi* and the smaller *Physa* and *Lymnaea* are much more difficult to detect in the process of opening the siphon since the sound produced is very faint or inaudible. In *H. campanulatum smithi* and *H. antrosom percarinatum*, the lung chamber does not project beyond the rim of the shell aperture, consequently, observations on breathing must be made by watching the general position of the respiratory opening which is located approximately above the head and beneath the rim of the shell aperture. *H. trivolvus* has been heard to open its respiratory aperture with a distinct click. However, it is done much less frequently in this species than in any of the larger Lymnaeidae and Physidae. The siphon of *L. emarginata angulata* is ordinarily extended through the surface film in the form of a cone, and the end of the aperture is opened so slowly that seldom is a distinct sound produced. The smaller *Lymnaea* and *Physa* have proportionally small respiratory openings and even though the breathing movements are closely similar with those of larger species, the sound produced by the opening of the pulmonary chamber is scarcely audible.

Inspiration.—Pauly (1877) states that time intervals between air breathing are dependent upon the directness or indirectness of course over which the snail travels to reach the surface. It is true that many snails take roundabout paths in reaching the top, yet, some snails may arrive in the same length of time as other individuals that travel a much shorter distance. Walter states that the "important factor appears to be not so much the distance to be traversed as the animal's need of oxygen and its response to food stimulus." A snail that is not suffering from the need of oxygen may pass in a leisurely manner to the surface of the water, feeding as it goes; whereas, an individual that has been deflated and has dropped to the floor of an aquarium will make a quick ascent regardless of the course over which it travels. Observations and experimental data show that the amount of air

inspired is one of the factors which determines the interval between breathing periods.

Walter states that the amount of air taken in by any individual is not necessarily dependent on the number of times the snail opens its siphon, but on the length of time the siphon remains open. It has been repeatedly observed that if a snail opens its aperture for a short interval (1-3 seconds) it will repeat the same process after closing the aperture sometimes as many as five or six times before making its way again to the bottom of the aquarium. Very frequently these short inhalations are terminated by a long one before the animal returns to its feeding. Again, the snail may come to the surface, immediately opens its aperture to what appears to be maximum distension and leaves it open for a period as long as 2.5 minutes (as observed in *L. palustris* and *L. stagnalis appressa*). After a long breathing period, the animal usually retracts its shell closely about the body and makes its descent into the deeper water. As observed by Walter, the approximate amount of air taken in can be demonstrated by the number of air bubble snails may be forced to release under water. This may be accomplished by the application of gentle pressure on the pulmonary sac with a small wooden probe.

Since Walter's statement that the amount of air inspired is dependent upon the inhalation period was not supported by experimental evidence a simple method was used to test the validity of his assumption. A single *L. stagnalis appressa* upon deflation, dropped to the bottom of the aquarium, and upon its return to the surface of the water, the inhalation period was timed. The animal was then deflated again and a record made of the number of air bubbles emitted. Since there is always a tendency for deflated snails, when reaching the surface, to open the aperture very wide and leave it open for a comparatively long period, the majority of the snails used in this experiment were induced to close their apertures by the expedient of gently touching the region near the pulmonary opening with a dissecting needle. Thus the time range of inhalation periods was secured. Data presented in table 2 were obtained from fifteen different specimens of *L. stagnalis appressa*.

From table 2 it is evident that there exists an apparent relation between the amount of air taken in and the period of inspiration. Individual number 11 failed to expand the aperture beyond a mere slit. This probably accounts for the small amount of air present in the pulmonary sac as compared to number 2 whose inhalation period was approximately the same yet released over twice the number of air bubbles as number 11. The size of the orifice probably plays an important role in governing the amount of air that enters the pulmonary chamber. The remaining snails expanded their apertures into circular openings the diameters of which varied considerably in the different individuals.

TABLE 2

SHOWING THE APPARENT RELATION OF THE INHALATION PERIOD OF *L. stagnalis appressa* TO THE AMOUNT OF AIR INSPIRED

No. of individual	Period of inhalation in seconds	Number of air bubbles released
1	2	2
2	49	25
3	8	8
4	15	9
5	118	31
6	17	10
7	5	4
8	10	8
9	70	27
10	50	20
11	42	10
12	84	30
13	17	12
14	106	32
15	35	21

Clessin (1877) and Roszkowski (1914) have both made statements to the effect that temperature may play an important part in the snail's need for air. Walter observed that "if snails were placed in a dish of water and exposed to direct sunlight," they would crawl up the sides of the dish and out of the water as the temperature was gradually raised. By packing an aquarium with ice, the movements of the snails become more sluggish. He also presented data on intervals between breathing, which show that two specimens of *L. palustris* ("*L. elodes*") visited the surface more frequently in water of higher temperatures. Although implying that the oxygen content of the water as well as temperature must be considered when explaining such movements, no specific data were given confirming this assumption.

It has long been known that fluctuations in temperature of water may be accompanied by changes in oxygen content. Such fluctuations may be of significance in changing the interval between breathing periods of snails. In order to determine the effect of different temperatures and different oxygen contents upon this interval, a series of experiments was conducted. Several battery jars of 1.3 liters capacity were filled with water of a known oxygen content and temperature. Since it was essential to use approximately the same weight of snail tissue in each battery jar, snails of each species were weighed and, after removal of the shells, the weight of the shells subtracted from the total weight. Table 3 gives the size range and number of individuals that closely equal 3.5 grams of soft parts.

Snails (one or more) having soft parts approximately equivalent to 3.5 grams weight were placed in each battery jar. In order to keep an accurate check on the number of trips individual snails made to the surface, the shell of each snail was given a distinguishing mark by means of white enamel paint. Such a method of marking proved very satisfactory in this and other

TABLE 3
NUMBER OF SNAILS APPROXIMATELY EQUIVALENT TO 3.5 GRAMS OF SOFT PARTS

Species	Diam. or height range of shells in mm.	Approx. no. of snails equiv. to 3.5 gm. soft parts
<i>L. emarginata angulata</i>	15-22 (height)	4
<i>L. palustris</i>	23-30 "	5
<i>L. stagnalis appressa</i>	40-48 "	1
<i>L. megasoma</i>	35-41 "	1
<i>P. sayii crassa</i>	8-11 "	23
<i>P. parkeri</i>	14-18 "	5
<i>H. antrosom percarinatum</i>	14-16 (diam.)	9
<i>H. campanulatum smithi</i>	15-16 "	8
<i>H. trivolvis</i>	19-23 "	6

experiments. Water of different temperatures and oxygen contents was obtained as follows: one group of experimental snails was transported to a small creek of fast-flowing water in which the temperature and oxygen content remained constant during the experiment. The snails were placed in battery jars which were filled with this water, and the jars in turn submerged in the creek to three-fourths their depth. Constant circulation of water around the sides of each container maintained a temperature of 11°C. within the jar. A second group of snails was put in lake surface water which had been cooled previously in the refrigeration room to a temperature of 12.5°C. During the course of the experiment, the temperature increased to 16.8°C. The third group of snails was placed in well water. This water, when first drawn from the well, was practically oxygenless, but due to the agitation in transportation from the well to the laboratory, and the time that elapsed before the beginning of the experiment, enough air had diffused into the water to bring the oxygen content up to 1.7 cc. per liter. The temperature of the water varied from 12.8°-20°C. inclusive during the experiment. A fourth group of snails was put in lake surface water. The temperature of the air in the laboratory was so similar to that of the water (21°C.) that no temperature change occurred during the course of the experiment. The fifth group of snails was placed in lake surface water which had been boiled, thus driving off most of the oxygen. However, after having cooled to a temperature of 28.8°C. when the experiment was begun, the oxygen content was 3.6 cc. per liter. The temperature fell from 28.8° to 24.4°C. during the course of the experiment. A maximum-minimum thermometer recorded the temperature range during each experiment. The amount of oxygen in the water at the beginning and termination of each individual experiment was determined by testing water of the same kind placed in battery jars as controls.

Tables 19-27 present the data obtained from this series of experiments. Temperature and oxygen ranges are also given. An analysis of these data leads to the following conclusions:

1. Breathing is a variable process since some snails, of the same species and in the same environmental surroundings, made several trips to the surface, whereas, others failed to visit the surface during the entire time they were under observation.

2. The average interval between breathing periods for all conditions of temperature and oxygen content varies in the different species, as shown in table 4. In considering the two extremes in table 4, the average interval

TABLE 4

VARIAION OF THE AVERAGE INTERVAL BETWEEN BREATHING PERIODS OF NINE SPECIES OF SNAILS (DATA FROM TABLES 19-27)

Species	Average interval in minutes
<i>L. palustris</i>	52.5
<i>L. stagnalis appressa</i>	62.6
<i>L. megasoma</i>	121.4
<i>H. trivolvis</i>	211.2
<i>P. parkeri</i>	304.9
<i>L. emarginata angulata</i>	325.7
<i>H. antrosom percarinatum</i>	513.9
<i>H. campanulatum smithi</i>	1368.2
<i>P. sayii crassa</i>	1493.0

between breathing periods for *P. sayii crassa* is approximately 29 times the interval for *L. palustris*.

3. That temperature of the water plays an important part in determining the average interval between breathing periods is clearly evidenced by data presented in table 5. The data presented in table 5 show that in water

TABLE 5

EFFECT OF TEMPERATURE ON THE INTERVAL BETWEEN BREATHING PERIODS (DATA FROM TABLES 19-27)

Species	Intervals between breathing periods in minutes	
	Temp., 11°C.; Oxygen 5.2 cc. per l.	Temp., 21°C.; Oxygen 6.1 cc. per l.
<i>L. palustris</i>	170.5	15.9
<i>L. stagnalis appressa</i>	216.0	31.0
<i>L. megasoma</i>	360.0	40.8
<i>H. trivolvis</i>	648.0	69.0
<i>L. emarginata angulata</i>	1080.0	165.6
<i>P. parkeri</i>	1080.0	98.8
<i>H. antrosom percarinatum</i>	2160.0	124.9
<i>H. campanulatum smithi</i>	6480.0	165.5
<i>P. sayii crassa</i>	6480.0	143.5
Average	2074.9	95.0

having a temperature of 11°C. the average interval between breathing periods for the 9 species is nearly 22 times that in water of 21°C. Not only is the difference between the oxygen content in the two series too small to

be significant but also both values (5.2 and 6.1 cc. per l) are far above the minimal requirement.

4. That the amount of oxygen present in water is an important factor in determining the interval between breathing periods is demonstrated when the average interval between breathing periods of snails in water of 6.4 cc. of oxygen per liter is compared with that in water having an oxygen content of 1.7 cc. per liter (table 6).

TABLE 6

EFFECT OF THE AMOUNT OF OXYGEN UPON THE AVERAGE INTERVAL BETWEEN BREATHING PERIODS (DATA FROM TABLES 19-27)

Species	Average interval in minutes	
	Temp. 12.5°-16.8°C.; Oxygen 6.4 cc. per l.	Temp. 12.8°-20° C.; Oxygen 1.7-2.6 cc. per l.
<i>L. palustris</i>	43.0	19.4
<i>L. stagnalis appressa</i>	44.3	11.6
<i>L. megasoma</i>	152.3	31.2
<i>H. trivolvis</i>	174.7	118.4
<i>H. antrosom percarinatum</i>	185.6	54.2
<i>H. campanulatum smithi</i>	186.1	63.4
<i>P. parkeri</i>	247.5	78.9
<i>L. emarginata angulata</i>	236.9	125.0
<i>P. sayii crassa</i>	660.0	144.8
Average	214.5	71.9

The data in table 6 show that in water having an oxygen content of 6.4 cc. per liter the average interval between breathing periods is approximately three times that in water with an oxygen content of 1.7 cc. per liter. Although the difference in the average interval is very significant, the well water used in obtaining the low oxygen content may have altered the normal behavior of the snails. However, if such was the case, it was not noticeable in their activity.

Oxygen Consumption

Although several authors have determined the respiratory quotients of various species of snails, such data concerning the fresh-water pulmonates are very meager. Hesse (1910) contributed the largest amount of information on the oxygen consumption of a single species of pulmonate snail. His work was done on *Helix pomatia*, one of the large terrestrial species. Hurst (1927) presented considerable data on the carbon dioxide elimination and oxygen consumption of *Physa occidentalis*. He compared the different respiratory exchanges of this species under different temperature conditions, and the different physiological states induced by parasitism. Borden (1931) furnished data on the oxygen consumption of *Planorbis corneus*. According to this author, the ability of that species to live in an environment deficient in oxygen is partly due to the reserve supply of oxygen in the

haemoglobin of its blood. So far as the writer is aware, no contributions have been made on the oxygen consumption of American lake pulmonates. The experiments and general discussion that follow are concerned with the oxygen consumption of snails which were subjected to different temperature conditions.

Method of determination.—In a selection of animals for oxygen consumption experiments several factors had to be considered. Borden (1931) pointed out an "apparent relationship between body weight and oxygen consumption" in *Planorbis corneus*. This author interprets the relationship as a "correlation between age and oxygen intake, the younger animals having a quicker metabolic rate." Hurst used weight as a measure of age in *Physa occidentalis*. He felt justified in establishing such a criterion, since, as he pointed out, "there is a limit to the size that may usually be reached and it is the exceptional individual that exceeds this." Out of the total population for each particular species, individuals were selected from the uppermost portion of the size range defined by the limits indicated in table 3. The writer feels that since the selection processes described below was the same for all species, all oxygen consumption values are therefore comparable.

Snails were removed from aquaria and the external surface of the shells dried with an absorbent cloth. They were then sorted in such a way that all individuals of each species were assembled in one group. Several individuals from each group were selected and weighed, care being taken that each group should not exceed 14 grams weight of soft tissue since that was the maximum weight of tissue placed in any one experimental bottle. The selection of this maximum weight value was arrived at by experimentation in the following manner. The approximate weight of the soft parts of a large *L. stagnalis appressa*, or *L. magasoma* is 3.5 gm. It seemed that four specimens of these large species with soft parts weighing 14 gm. might be placed in a 0.4 liter bottle without apparent crowding of the individuals. But the question arose as to whether or not the average oxygen consumption per gram weight of soft parts per hour would be approximately the same for four snails, all of the same species, when placed in one bottle, as it would be for four individual snails of the same species placed in separate bottles. Since no significant difference occurred (table 37) in the average values of the two conditions, evidently the excretory wastes from the four snails in one bottle did not lower their metabolic rate, and consequently the results obtained would be indicative of snails under normal conditions. Such comparative averages were determined only for the larger species (*L. magasoma*, *L. stagnalis appressa*, *L. emarginata angulata*, *H. trivolvis*, *P. parkeri*, and *L. palustris*), since in the smaller species (*P. sayii crassa*, *H. antrosom percarinatum* and *H. campanulatum smithi*), the maximum weight of soft parts placed in any one bottle seldom exceeded 6 or 7 grams. The comparative

averages determined for each species of snail, tested under the described conditions, were so nearly alike, it was evident that as much as 14 grams of soft parts of the species tested could be placed in one experimental bottle without interfering with the normal metabolism of the snails during each experiment. Individuals of each group of snails were then deflated and placed in 0.4 liter, wide-mouth bottles which had been filled with surface lake water. These bottles were then tightly stoppered under water to exclude air bubbles.

The oxygen content of the lake water used was determined at the beginning of each experiment. A control bottle filled with water from the same source and tightly stoppered stood for the same duration, and under the same temperature conditions as the experimental bottles. A maximum-minimum thermometer, placed in an open vessel of lake water, recorded the range of temperature during the course of the experiment. At the termination of each experiment, the oxygen content of the water in each experimental bottle, as well as in the control, was again determined and the amount present in the experimental bottle subtracted from the oxygen content of the control. The result so obtained represented the oxygen extracted from the water by the snails in a definite period of time. Since there is animal and plant life in the lake water which uses up oxygen, this feature was taken into consideration in calculating the amount of oxygen used by snail life alone as follows: a great deal of the oxygen loss due to consumption by animal and plant life is partly compensated for by the oxygen production by chlorophyll-bearing algae during the day. Since the water in the experimental and control bottles was from the same source, this consumption and production of oxygen due to microscopic organisms in the water should be essentially the same in the two bottles. Therefore, a satisfactory determination of the oxygen consumed by snail life alone was made by subtracting the amount present in the experimental bottle at the termination of the experiment from the amount present in the control. All oxygen determinations in this set of experiments were made by the Micro-Winkler method. After determining the amount of oxygen used by each group of snails, these animals were killed in boiling water, and their extended bodies removed from the shells. The shells were dried with an absorbent cloth; weighed; and the weight of the shells from each group of snails subtracted from the original weight of the group (shells plus soft parts) which gave the exact weight of soft parts. By dividing the amount of oxygen consumed by the number of grams of soft parts, and dividing this quotient by the duration of the experiment (in hours), the resulting figure is the average oxygen consumption per gram weight per hour.

Effect of temperature.—Vernon (1895) made a careful study of the respiratory exchanges at different temperatures of a number of different marine invertebrates and prochordates. He showed that changes of temper-

ature exert a marked influence on the rate at which oxygen is absorbed, and found that certain species in water at 24°C. consume at least twice as much oxygen as at 10°C. In a few species, the amount of oxygen absorbed at the higher temperature was more than four times the amount absorbed at the lower temperature. Hurst's results on the oxygen consumption of *P. occidentalis* in fall and winter conditions show that the amount of oxygen consumed in water at a temperature of approximately 21°C. is nearly twice that absorbed at 4°C.

Tables 28-36 inclusive present the data obtained from nine species of snails submerged under different temperature conditions. In experiments conducted in the laboratory, the extreme temperature variation was 14.5°-32°C. In order to obtain the necessary low temperatures, a refrigeration room maintaining a constant temperature of 5.5°C. was used. Since in the early part of the work it was discovered that many snails cannot survive the direct shock of being introduced from warm water (29.4°C.) to cold water (5.5°C.), all snails were cooled gradually by introducing them into the refrigeration room in aquaria containing water at laboratory temperatures. Approximately 24 hours were required to cool the warm aquarium water down to the temperature of the refrigeration room.

An examination of tables 28-36 inclusive shows that in water at room temperatures there is a decided difference in the average amount of oxygen absorbed by different species of snails in a given time. Table 7 gives the average amount of oxygen consumed by each of the nine species at room temperatures. Since the extreme variation of temperature (14.5°-32°C.; day-night) was effective simultaneously in all species, the results are comparable.

TABLE 7

OXYGEN CONSUMPTION AT ROOM TEMPERATURES (14.5°-32°C.) (DATA FROM TABLES 28-36)

Species	Average oxygen consumption in cc. per gm. wt. per hr.
<i>L. palustris</i>	0.03874
<i>L. megasoma</i>	0.03332
<i>L. stagnalis appressa</i>	0.02960
<i>H. trivolvis</i>	0.01300
<i>P. parkeri</i>	0.01199
<i>L. emarginata angulata</i>	0.01141
<i>H. campanulatum smithi</i>	0.00973
<i>H. antrosom percarinatum</i>	0.00842
<i>P. sayii crassa</i>	0.00581

From the data presented in table 7 it is seen that the swamp species, *L. palustris* and *L. megasoma*, absorb approximately six times the amount of oxygen per gram weight of soft parts consumed by *P. sayii crassa*, an inhabitant of the exposed areas on Douglas Lake. *L. stagnalis appressa* also uses approximately four times as much oxygen per gram weight of soft parts

as does *P. sayii crassa*. The average oxygen consumption of healthy *P. occidentalis* for fall, winter, and spring temperatures (Hurst, 1927) is in all instances higher than the oxygen consumption of Douglas Lake pulmonates. This difference, however, is not unexpected since the activities of most snails inhabiting ponds, small streams, and swamps, are much greater than the activities of lake pulmonates. For example, the average oxygen consumption of *L. palustris*, a typical swamp snail, closely approximates that of *P. occidentalis* under low as well as high temperatures. *H. trivolvis*, a relatively sluggish form, has an oxygen consumption that agrees rather closely with the larger individuals of *Planorbis corneus* as reported by Borden (1931). Both species are very closely related and occur in similar habitats. Hurst considered the difference in the amount of oxygen consumed per gram weight of tissue by *P. occidentalis* and by *Helix pomatia* to be due to the smaller size and greater activity of the former. As previously mentioned, the more active the animal, the greater the amount of oxygen consumed. However, size cannot always be used to explain why certain species of snails consume more oxygen than others. In direct contrast to the rather large amount of oxygen absorbed by *P. occidentalis* compared to *H. pomatia*, *P. sayii crassa* (the smallest species used in this work) consumed less oxygen per gram weight of tissue than any other species. Slow and sluggish movements of this animal in its natural habitat compared to the much greater activity of *P. occidentalis* probably accounts for the major difference in the amounts of oxygen consumed by these two species.

An examination of the interval between breathing periods and the oxygen consumption showed a definite correlation of the two activities. In table 8, the different species are arranged according to the average interval between breathing periods.

TABLE 8
CORRELATION OF AVERAGE INTERVAL BETWEEN BREATHING PERIODS AND OXYGEN CONSUMPTION

Species	Average interval in min.	Average oxygen consumption in cc. per gm. wt. per hour
<i>L. palustris</i>	52.5	0.03874
<i>L. stagnalis appressa</i>	62.6	0.02960
<i>L. megasoma</i>	121.4	0.03329
<i>H. trivolvis</i>	211.2	0.01300
<i>P. parkeri</i>	304.9	0.01199
<i>L. emarginata angulata</i>	325.7	0.01141
<i>H. antrosomum percarinatum</i>	513.9	0.00842
<i>H. campanulatum smithi</i>	1388.2	0.00973
<i>P. sayii crassa</i>	1493.0	0.00581

This correlation (table 8) is rather striking for all 9 species. Slight deviation occurs in *L. megasoma* which, judged from the oxygen consumption

should theoretically follow *L. palustris*, and, *H. campanulatum smithi* which should theoretically follow *L. emarginata angulata*. Causes of these deviations are unknown.

The effect of low temperatures on the amount of oxygen absorbed by the different species is very evident if one compares the amounts consumed in room temperatures with those consumed in a low temperature (table 9.)

TABLE 9
OXYGEN CONSUMPTION AT ROOM TEMPERATURES AND LOW TEMPERATURE
(DATA FROM TABLES 28-36)

Species	Average oxygen consumption in cc. per gm. wt. of soft parts per hour	
	Room temps. (14.5°-32.0°C.)	Low temp. (5.5°C.)
<i>L. palustris</i>	0.03874	0.01090
<i>L. megasoma</i>	0.03329	0.01653
<i>L. stagnalis appressa</i>	0.02960	0.00849
<i>H. trivolvis</i>	0.01300	0.00299
<i>P. parkeri</i>	0.01199	0.00551
<i>H. campanulatum smithi</i>	0.00973	0.00314
<i>L. emarginata angulata</i>	0.01141	0.00354
<i>H. antrosom percarinatum</i>	0.00842	0.00271
<i>P. sayii crassa</i>	0.00581	0.00079

The data in table 9 show that a low temperature influences, to a considerable extent, the amount of oxygen consumed by each of the nine species. *L. megasoma* is affected less by the temperature change than is any other species. In water at room temperature, the oxygen consumption in this species is only approximately twice that at 5.5°C. However, in *P. sayii crassa*, which exhibits the greatest relative difference in oxygen consumption under the two conditions, the oxygen intake at room temperature is more than seven times that at 5.5°C. Therefore, it is clear that each species of snail manifests a physiological individuality.

SUBMERGENCE

Natural Submergence.—The ability of certain aquatic pulmonates to live submerged for long periods of time has been observed by many investigators. Several European, American, and Japanese workers have dredged pulmonate snails from such great depths in fresh-water lakes that it would be impossible for any of them to reach the surface by their own locomotion. Thus they must spend their entire existence without access to atmospheric air.

Table 10 lists a few of the more exceptional records of pulmonate snails dredged from the depths in fresh-water lakes.

TABLE 10
DEPTH RECORDS OF PULMONATE SNAILS

Observer	Locality	Species	Remarks
Forel (1869)	Lake Geneva	" <i>L. stagnalis</i> "	250 m. Pulmonary sac full of water
" "	Lake Constance	" <i>L. abyssicola</i> "	" " "
Siebold (1875)	Lake Constance	" <i>L. abyssicola</i> "	70 m.
Pauly (1877)	Starnbergersee	" <i>Lymnaea</i> sp."	15 and 25 m.
" "	"	" <i>L. auricularia trimica</i> "	" " "
" "	"	" <i>L. stagnalis</i> "	" " "
Andre (1901)	Lake Geneva	" <i>L. auricularia con-</i> <i>tracta</i> "	40 m.
Roszkowski (1914)	Lake Geneva	" <i>L. ovata profunda</i> "	100 m.
" "	"	" <i>L. palustris abyssi-</i> <i>cola</i> "	100 m.
Miyadi and Hazama (1932)	Lake Yogo	" <i>Gyraulus japonicus</i> "	5-7 m. 10.4 per sq. m.
Walker (1900)	Crystal Lake, Mich.	" <i>L. mighelsi</i> "	3.6 m. down and none on surface
Kirkland (1900)	Crystal Lake, Mich.	" <i>L. emarginata angu-</i> <i>lata</i> "	3.6 m. in July
Eggleton (1931)	Douglas Lake, Mich.	" <i>Planorbis altissimus</i> "	10-12 m.
" "	" "	" <i>Planorbis parvus</i> "	4-10 m.
" "	Kirkville Green Lake, N. Y.	" <i>Planorbis antrosus</i> <i>striatus</i> "	1-5 m.
Baker, H. B. (1911)	Saginaw Bay, Lake Mich.	" <i>Planorbis bicarinatus</i> "	4.8-7.3 m.
" "	"	" <i>Physa ancillaria</i> "	" "
Smith and Verill (1871)	Lake Superior	" <i>Limnaea</i> sp."	14.5-24 m.
" "	"	" <i>Physa heterotropha</i> "	" "
" "	"	" <i>Physa vinosa</i> "	11-14.6 m.
" "	"	" <i>Planorbis parvus</i> "	14.5-24 m.
Smith (1874)	Lake Superior	" <i>Limnaea lanceata</i> "	18-36.5 m.
" "	"	" <i>Physa ancillaria</i> "	" "
" "	"	" <i>Physa heterotropha</i> "	" "
" "	"	" <i>Gyraulus parvus</i> "	" "
Muttkowski (1918)	Lake Mendota, Wis.	" <i>Physa gyrina</i> "	4.8-7 m. 11.4 per sq. m.
" "	"	" <i>Planorbis bicarina-</i> <i>tus</i> "	4.8-7 m. 75.4 per sq. m.
" "	"	" <i>Planorbis campanu-</i> <i>latus</i> "	4.8-7 m. 21.7 per sq. m.
" "	"	" <i>Planorbis parvus</i> "	4.8-7 m. 33.7 per sq. m.
Adamstone (1923)	Lake Nipigon, Ont., Canada	" <i>Planorbis parvus</i> ."	15.2 m.
" "	"	" <i>Planorbis antrosus</i> "	8.2 m.
Scott, Hile, and Spieth (1928)	Lake Wawasee, Ind.	" <i>Planorbis</i> sp."	4.8 m. Max. popula- tion
Walker (1896)	Lake Mich.	" <i>Limnaea</i> sp."	25 m.
" "	"	" <i>Planorbis</i> sp."	25 m.
Wright (1929, un- published)	Lake Erie	" <i>Helisoma trivolvis</i> ."	11.8 m. 1 per sq. m.
" "	"	" <i>Physa magnalacus-</i> <i>tris</i> ."	14 m.

In many cases, such records are unaccompanied by chemical data. This leaves one largely in the dark respecting the actual environmental conditions under which such snails live. Forel (1869) and Brot (1877), in investigating "*Lymnaea abyssicola*," found that the pulmonary chamber of this species contained no gas at the time it was taken from the water, but,

when placed in a jar of water, it immediately came to the surface and behaved similarly to its shallow water relatives. Pauly suggested that those *Lymnaea* living at great depths in lakes may retain the primitive use of the lung in securing oxygen from the water as in the case of all young *Lymnaea* for a considerable period after being hatched. Roszkowski (1914), in his extensive work on the profundal *Lymnaea* of Lake Geneva, found the lung of all individuals filled with water. He interpreted this condition as a return to the branchiate type of respiration, thus constituting an adaptation for abyssal life. Walter suggests that this may possibly be regarded as evidence of a physiological reversion to an ancestral condition, since the pulmonates are more recent phylogenetically than the gill-breathing gastropods. He adds, however, that "breathing without coming to the surface at all may in the case of pulmonates be considered as abnormal breathing."

Many of the cases cited in table 10 are snails which dwell at so great a depth that visits to the surface are practically impossible. Pauly explains the breathing behavior of those snails which dwell in shallow water but make no attempt to reach the surface by stating that they capture free air from bubbles entangled below the surface on vegetation and other objects, basing this conclusion on his own observation in which he actually saw the snails approach such bubbles and suck the air from them into the respiratory chamber. However, the experiences of the writer agree with Walter's observations in that he has never seen pulmonate snails use the method described by Pauly in securing air. While the Pauly statement may at first thought seem probable, yet representatives of all nine species of snails used in this work have been put into aquaria in which abundant vegetation was present and then the aquaria placed in sunlight to insure plenty of photosynthetic action. Plants under such conditions have been almost covered with small bubbles of oxygen, and yet, after hours of observation, no snail has ever been seen to actually use this gas directly as a source of oxygen supply. It has been observed, however, that snails in aquaria in which vegetation is present make fewer trips to the surface than do those in aquaria which lack vegetation. This behavior can probably be explained by assuming that in such a situation the water is saturated with oxygen and through cutaneous respiration sufficient oxygen is absorbed to supplement the pulmonary breathing. Hence, the number of trips to the surface in a given time would be less under such conditions than in water which is much lower in oxygen content.

Experimental submergence.—Pauly was successful in keeping an experimentally submerged *L. stagnalis* alive for 91 days, and in this individual as well as several others that were submerged under similar conditions, air was not allowed to enter the lung cavity. Thus he concluded that in such instances respiration was accomplished through the skin and not by the lung. Several instances are on record of snails that have been denied

access to atmospheric air and since these records are pertinent to this discussion they are given in table 11.

TABLE 11
SURVIVAL PERIODS OF ARTIFICIALLY SUBMERGED SNAILS

Observer	Species	Survival period in days
Saint-Simon (1853)	" <i>Physa</i> sp."	4
" " "	" <i>Planorbis contortus</i> "	12
Moquin-Tandon (1855)	" <i>Ancylus</i> sp."	13
" " "	" <i>Planorbis leucostoma</i> "	18
" " "	" <i>Lymnaeus elongatus</i> "	19
Pauly (1877)	" <i>Lymnaea stagnalis</i> "	91
" " "	" " "	22
Walter (1906)	" <i>Lymnaea elodes</i> "	4

Walter's experiments on artificial submergence of *L. palustris* ("*L. elodes*") yielded, for the most part, negative results. Out of a large group of snails placed in a tub directly under the inflow of fresh water, several survived for 4 days (table 11). From this experiment he concluded that, "in certain conditions where much free air is driven into the water in the form of bubbles, water pulmonates are able either to reduce the number of their journeys to the surface to a minimum or to dispense with them altogether." He added, however, that "this is only a modification of surface breathing, involving no real functional adaptation. In such cases death ensues prematurely and the inability of the snail to adapt itself suddenly to extracting its air supply from water alone is clearly demonstrated."

Since it has been demonstrated that low temperatures influence, to a large extent, the amount of oxygen absorbed by all nine species of snails, the question then arises as to what effect low temperatures have on prolonging the lives of snails forcibly submerged. With this question in mind, the following experiments were conducted.

Situated within three-fourths of a mile from the University of Michigan Biological Station is a small creek (Carp Creek) that has as its source seepage water from Douglas Lake. This creek drains into Burt Lake, and at its entrance into the latter, widens, thus forming a small delta (fig. 20). At this delta, a temperature gradient is formed by the cold water of the creek gradually mingling with the warm water of the lake. By the selection of certain sites near the source of this stream, in the delta, and in the lake, a series of temperatures was obtained which varied from 11° to 25.5°C. Four of these sites were selected for experimental work and were designated as follows:

Station 1.—Situated near the source of the stream; temperature closely approximating 11°C. throughout the summer.

Station 2.—Located at the narrow end of the delta (fig. 20, a); temperature variation during the course of the experiment was 12.2°–16.6°C.

Station 3.—Situated at the wide end of the delta (fig. 20, b); temperature variation 13.3° – 21.6° C.

Station 4.—Situated in the open lake; temperature variation, 21.6° – 25.5° C.



FIG. 20. Entrance of Carp Creek into Burt Lake

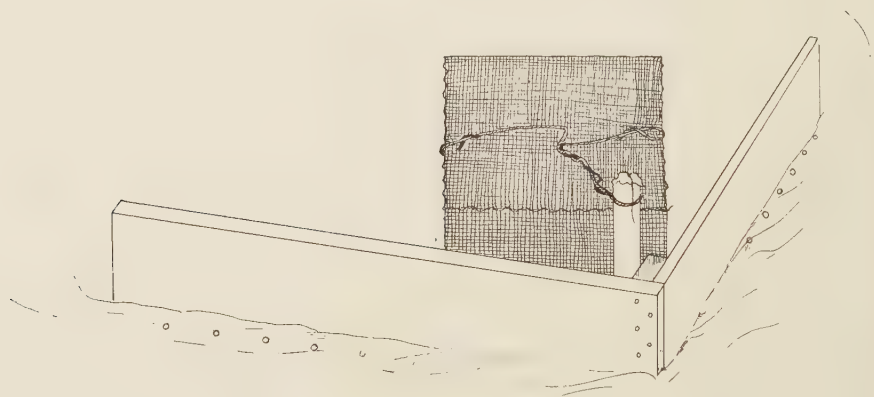


FIG. 21. Deflector used in Carp Creek to prevent sand from covering cages, and to produce quiescent condition for snails in cages

The fluctuation in temperature in stations 2 and 3 was due largely to wave action on the lake. On certain days, an offshore wind drove the surface lake water away from the creek, so that the deeper, cooler water

of the lake rose at that position and mingled with the creek water, lowering the temperature of water in the delta. On other occasions, an onshore wind drove the warmer surface water of the lake into the delta of the creek thus increasing the temperature. A maximum-minimum thermometer at each station recorded the range of temperature during the course of the experiment. Due to the rapid current in the creek, and consequent shifting of sand, it was impossible to place exposed cages anywhere in the creek without the danger of them being completely buried by sand within one or two days. In order to avoid most of this difficulty, and at the same time produce a fairly quiescent condition of water for the submerged snails, deflectors (fig. 21) were made as follows: two boards, each 1×0.5 meters were placed on edge and nailed together at right angles, thus forming two wings. Six 1.5 centimeter holes, space 5 centimeters apart, were bored from the free end of each wing along the middle and toward the apex. These holes allowed currents of water to pass through the deflector. These currents were sufficient to wash away most of the sand that tended to encroach inward from the ends. Each deflector was then nailed to a stake and this stake driven deep into the sand, at the chosen site, in such a manner that the apex of the deflector headed into the current. Two wire cages (20x25x25 centimeters) were placed behind each deflector. The cage containing the experimental animals was completely submerged, while the other cage containing the control animals was placed on top of it, being about one-half submerged. This allowed the control animals access to the surface. Although the deflectors prevented a rapid accumulation of current-borne sand from covering the submerged cage, it was nevertheless necessary to remove once each week the sand that piled up around the cages.

Representatives of the nine species of snails were used in this experiment. Twelve specimens of each species were selected for use in each set up. In each experimental cage, six individuals of each of the nine species were deflated before submergence and the shells marked with white enamel. The remaining snails were submerged with air present in the pulmonary sac. Before the snails were placed in station 1 and 2 where the water was rather cold, they were gradually acclimated in the same manner as described on page 368. All experimental and control snails were fed lettuce leaves and apple once a week. Table 38 presents the data obtained from this experiment.

The data in table 38 show the following:

1. In station 1 with the lowest temperature ($11^{\circ}\text{C}.$), the total per cent of all species of snails surviving was more than three times as high as the total per cent surviving in station 4 with the highest temperature (21.6° – $25.5^{\circ}\text{C}.$).

2. The mortality among these species whose oxygen consumption is the highest was much greater than among those species with a lower oxy-

gen consumption. In station 4, *L. palustris* and *L. megasoma* all died before the experiment was terminated, whereas several *P. sayii crassa*, *H. antrosom percarinatum*, and *H. campanulatum smithi* survived the 62 days of submergence.

3. Survival was higher in snails that were submerged with air present in the pulmonary chamber. This may be due to the inability of some snails to suddenly adapt themselves wholly to cutaneous respiration.

4. Some individuals of each of the nine species represented withstood direct submergence for periods as long as 62 days in the lower temperatures. Since it has been demonstrated that low temperature reduces, to a considerable extent, the amount of oxygen consumed by the snails (pp. 36-37), it would seem that an explanation for the ability of all nine species to survive at low temperature may be postulated as follows: the temperature of the surrounding water was low enough to reduce the oxygen consumption of these individuals to such an extent that an amount sufficient to maintain their body needs was respired cutaneously.

At the termination of this period of experimental submergence, all surviving snails were tested for the presence of air in the pulmonary chamber. In all cases, air was absent, and the pulmonary sac filled with water. Such a condition is in direct contrast to Pauly's findings namely, in a *L. stagnalis* submerged for 91 days air was not allowed to enter the pulmonary chamber. The presence of water in the pulmonary chamber brings about a condition similar to that found in abyssal snails whose pulmonary chambers are always filled with water. Presumably, the lung functions similarly to a gill under such conditions.

In order to determine what effect if any submergence in a vegetation zone would have on prolonging the life of submerged snails, the following experiment was performed.

Two wire cages were constructed, each one having the dimensions of 1x1x2 meters. Both cages were made of galvanized mesh wire (2.6 inches per sq. centimeter) and divided into two equal compartments by a partition made of the same material. The cages were supported in wooden frames and, when submerged, were anchored by weights attached to the lower corners. Forty-eight snails of each of the nine species were used. Of this group, 24 individuals of each species were marked with white enamel and deflated. Twelve of the 24 were placed in a compartment of one cage, and the remaining 12 in a compartment of the other cage. The same number of non-deflated snails was placed in the two remaining compartments of the cages. Thus, each of the two cages had 108 (12 snails of each of the 9 species) deflated snails in one compartment and the same number of non-deflated snails in the other compartment. One cage was then submerged in a vegetation zone consisting most of *Potamogeton*, *Elodea*, and *Myriophyllum*; the other in an exposed, vegetationless zone. Both cages were sub-

merged in water approximately 3 meters in depth. The experiment extended through a period of 65 days and during that interval the surface temperature of lake water varied from 16.8° to 26.6°C. Table 12 presents the data obtained.

TABLE 12

NUMBER OF DEFLATED AND NON-DEFLATED SNAILS SURVIVING 65 DAYS OF EXPERIMENTAL SUBMERGENCE IN VEGETATION AND EXPOSED ZONES. IN EACH INSTANCE, THE ORIGINAL GROUP CONSISTED OF 12 SNAILS
(TEMP. RANGE 16.8°-26.6°C.)

Species	Number surviving				Percent of total no. surv.
	Veget. zone		Exposed Zone		
	Non-defl.	Defl.	Non-defl.	Defl.	
<i>L. palustris</i>	0	0	0	0	0.0
<i>L. megasoma</i>	1	0	0	0	2.08
<i>L. stagnalis appressa</i>	3	0	4	1	16.67
<i>L. emarginata angulata</i>	2	1	4	2	18.75
<i>P. parkeri</i>	2	0	5	1	16.67
<i>P. sayii crassa</i>	3	3	7	5	37.50
<i>H. trivolvis</i>	5	1	2	0	16.67
<i>H. campanulatum smithi</i>	6	0	5	3	29.17
<i>H. antrosom percarinatum</i>	4	0	8	2	29.17
Total	26	5	35	14	

The results obtained from submergence in these two zones show that the number of surviving snails of most species is higher on the exposed shoal than in the plant zone. Of the total number of all species submerged in the vegetation zone, 14.3 per cent survived, whereas 22.6 per cent survived in the exposed zone. It is of interest to note that snails which occur most abundantly along an exposed shore show a greater survival when submerged in such a habitat than they do when submerged in a vegetation zone. In *H. trivolvis*, a species which is associated more often with quiet water in vegetation areas, the number surviving was higher in the vegetation zone. Such results appear to indicate that the active photosynthetic littoral zone of a lake did not increase the number surviving of submerged snails, deflated or non-deflated. Even though forcibly submerged, the environment to which each species of snail is accustomed plays a more important part in the number surviving than does a zone rich in plant life. As was demonstrated in the Carp Creek experiment, the number of deflated snails surviving was much less than that of non-deflated individuals.

ANNUAL MIGRATORY CYCLE

It is a well known fact that many forms of animal life undergo periodic movements in their environment. These movements or migrations are largely influenced by certain physico-chemical changes occurring in that

environment which act directly or indirectly on the physiological processes of the organism. The fresh-water snails exhibit such behavior and will be discussed here with special regard to the lake species. The exact information obtained on local distribution and on the presence or absence of air in the pulmonary chamber was made possible by the use of a diving helmet.

AREAS STUDIED

Douglas Lake.—During the course of this work, three areas on Douglas Lake that represented rather unique and contrasting environmental situa-



FIG. 22. Grapevine Point habitat

tions were kept under close observation. Since each of these habitats possessed certain environmental factors that were conducive to the growth propagation of certain species of snails and yet did not entirely eliminate other species, an excellent opportunity was afforded for a comparative distribution study with regard to the physical features of a lake environment.

The Grapevine Point area (figs. 22–23) is characterized by a sand shelf with medium slope extending 110 meters into the lake from the water's edge. The depth of the water varies from 0 to 5.5 meters. Due to the exposure of this shelf to wind and the resulting wave action (fig. 22) from a large, open expanse of lake, the area is practically devoid of plant life. The sand bottom, however, is strewn with pebbles and boulders which afford some protection to the snails.

The Hook Point habitat (figs. 24-25) presents a striking contrast to that on Grapevine Point. Instead of being exposed, it is well protected from severe wave action. The water is usually quiet and conditions are such that aquatic vegetation of the genera *Potamogeton*, *Myriophyllum*, *Elodea*, *Sparganium*, and *Chara* flourishes (fig. 24). The slope instead of being a gentle one is very abrupt. Within a distance of 18 meters, the narrow shelf declines abruptly into water 5.5 meters deep. This very narrow sand and marl shelf which is covered with abundant vegetation affords admirable protection for mollusks.

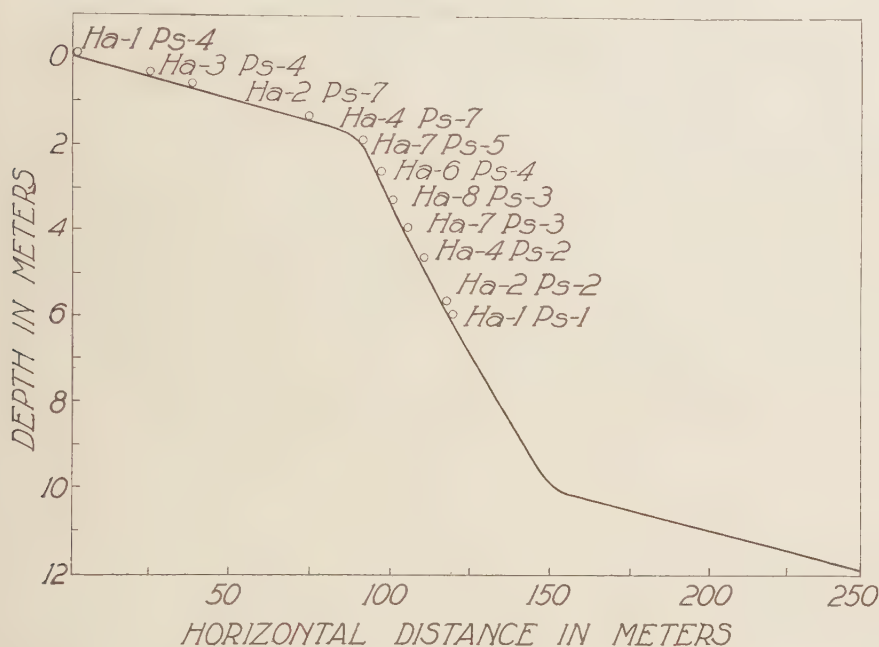


FIG. 23. Profile of Grapevine Point shoal showing distribution of snails per square meter.

Ha—*Helisoma antrosom percarinatum*

Ps—*Physa sayii crassa*

The Ingleside area (figs. 26-27) is characterized by the widest and most gradual slope of any of the three habitats. Extending from the shore line a distance of 250 meters into the lake, the depth varies from 0 to 1 meter. Due to the protection from heavy wave action in this small bay, vegetation is encroaching from the shore line into the open water of the lake. Such a region provides an excellent breeding and foraging substratum for snails.

Other regions.—Several other regions have been studied with special regard to distribution in relation to water temperatures. A thriving colony of *L. columella* in a small lake approximately 12 miles southwest of Ann

Arbor, Michigan, was kept under observation during the fall, winter, and spring months of 1930, 1931 and 1932. Several small streams and woodland pools near Ann Arbor, Michigan, were also under close observation during the same period. A trip was made, during the late summer of 1932, to various lakes in Keweenaw County, Upper Peninsula, Michigan.



FIG. 24. Hook Point habitat.

DISTRIBUTION

Relation to temperature.—It has been known for a long time that temperature plays a very important part in the distribution of animals. It is also well known that not all poikilothermic animals undergo a period of dormancy. Some of these organisms migrate to avoid low temperatures. Such migrations may be of local nature or over large geographic areas. Fresh-water pulmonates belong among those animals which make local migrations to avoid low temperatures, and do not undergo a period of dormancy unless environmental conditions necessitate it.

The relation of temperature to the migration of these animals was first brought to the writer's attention by several field observations on a rather deep pool which was heavily populated with *Physa* and a small lymnaeid snail. These observations were made during the fall, winter, and spring months, when the water in the pool was subjected to rather abrupt changes in temperature due to the fluctuating air temperatures. On warm days when the temperature rose from 10° to 18° or 21°C., snails were always abundant on the surface. However a few cold days which lowered the temperature from 21° to 10°C. invariably produced a general migration of

these animals from the surface to the deeper water. The snails remained in the deeper water as long as the cold weather lasted, but, when the water was warmed up by several days of higher temperature, they had again moved to the surface. A simple experiment was carried out in order to test the reaction of laboratory-reared snails to changes in temperature. An aquarium containing water at room temperature (25.5°C.) and snails of the genera *Lymnaea*, *Physa*, and *Helisoma* was placed on an outside window ledge thus exposing it to low winter temperatures. At the time the aquarium

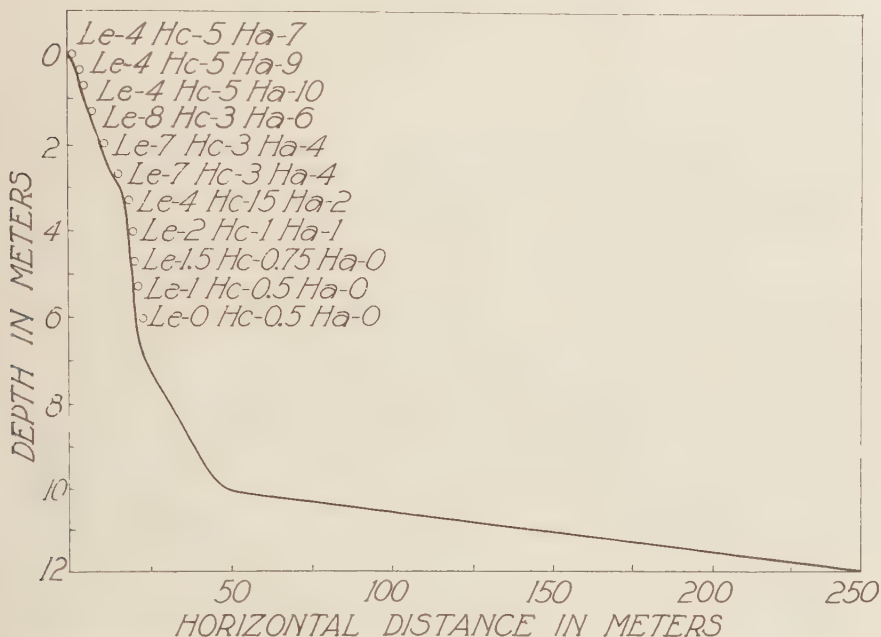


FIG. 25. Profile of Hook Point shoal showing distribution of snails per square meter.

Le—*Lymnaea emarginata angulata*

Hc—*Helisoma campanulatum smithi*

Ha—*Helisoma antrosom percarinatum*

was placed outdoors, practically all of the snails were at or near the surface. Within 48 hours, the water had cooled from 25.5° to 10°C., and accompanying this temperature decrease was a decided migration from the surface to the deeper water. Many such experiments were subsequently performed, using, in all, over 16 species of pulmonates. The results were invariably the same, namely, low temperatures produced a migration from the surface downward, whereas the high temperatures caused an ascent to the surface.

It is a well known fact, that after the water has warmed up in the early summer, pulmonates appear abundantly in the shallows. An examination of these same regions shortly after the ice breaks up in the spring reveals few or no snails. In autumn as long as the water remains fairly warm (18° – 25.5° C.), snails may occur abundantly in the littoral region of the lake. But, accompanying the temperature decline to the freezing point is a gradual disappearance of snails in the shallows due to a migration into the deeper and better protected regions.



FIG. 26. Ingleside habitat

Thus a temperature change of sufficient magnitude appears to be the stimulus for migration of fresh-water pulmonates. The migration to deeper water in the fall enables them to avoid the inevitable adverse conditions of the littoral region in winter. When they have migrated to the deeper water of the lake, they are very sluggish due to the low temperature, but are nevertheless active to a certain extent throughout the winter and early spring months when the lake is frozen over. This is a group of organisms which, although equipped with facilities for breathing atmospheric air, spends at least three or four months out of every twelve naturally submerged. During this entire period such snails do not have access to air and, consequently, must rely altogether on their ability to extract oxygen

directly from the water. In tracing the annual migratory cycle of snails in Douglas Lake, the following seasonal distribution occurred.

By the latter part of June, many of the snails in Douglas Lake have completed their migration from the deeper to the shallower water. Arrival in the littoral zone is not uniform for all species. Those lake pulmonates whose oxygen consumption is highest (*L. stagnalis appressa*, *H. trivolvis*, and *P. parkeri*) are the first to appear in shallow water. Their demands for oxygen other than that extracted directly from the water, are much greater than those of the species (*L. emarginata angulata*, *H. campanulatum smithi*, *H.*

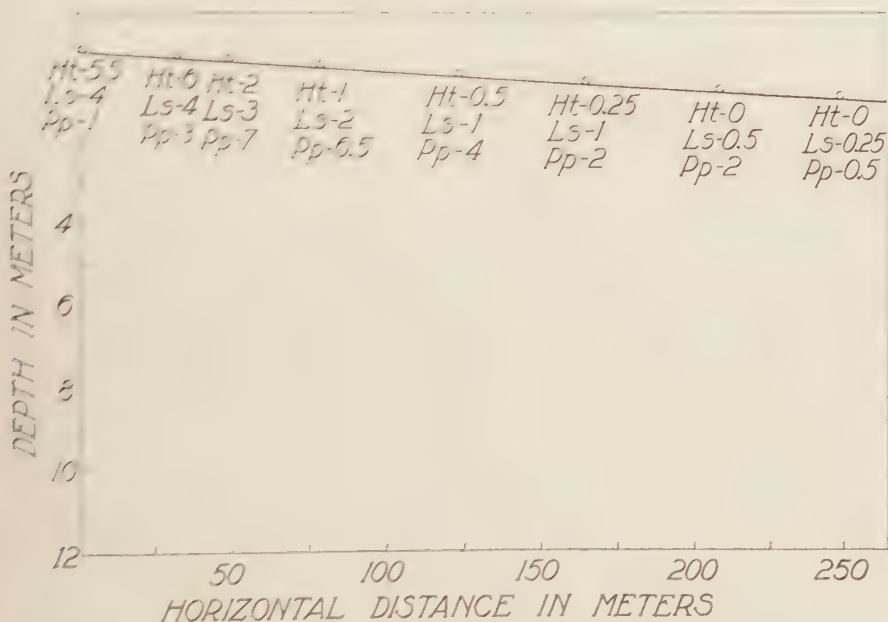


FIG. 27. Profile of Ingleside shoal showing distribution of snails per square meter.

Ht—*Helisoma trivolvis*

Ls—*Lymnaea stagnalis appressa*

Pp—*Physa parkeri*

antrocom percarinatum, and *P. sayii crassa*) whose oxygen consumption is lower.

It is true that some individuals of each of the seven species of pulmonates inhabiting Douglas Lake fail to complete their migratory journey to the surface during the course of the summer and early fall months. It has been proved by experimental submergence that individuals representing 7 species of lake pulmonates can survive at least for 65 days (table 12) submerged in lake water at summer temperatures (16.6°–26.6°C.). The sur-

vival number for those snails with a much lower oxygen consumption is greater than for those species whose oxygen consumption is higher. Since the oxygen demand of those snails that fail to reach the surface during the summer months is comparatively low, it would not seem unusual to find these snails lagging behind in their migratory cycle.

During the months of August and September, 1932, a general census of the distribution of pulmonate snails was made in three habitats on Douglas Lake which were kept under close observation during the course of this work. By the use of a wire frame, enclosing one square meter, and of a diving helmet, the average number of snails per square meter was determined at various depths at each habitat from the water's edge directly out in the lake to a distance of at least 122 meters. At each of the selected depths, the snails were counted in two square meters and the average number computed for one square meter (figs. 23, 25, 27).

At Grapevine Point, the maximum population (fig. 23) of *H. antrosom percarinatum* occurred at a depth of 3 meters. The majority of the snails at that depth had their heads directed shoreward, and in all the snails examined, the pulmonary sacs were filled with water. Since the floor of the lake in this habitat was vegetationless and covered with hard packed sand which increased the reflection of light rays, visibility at depths of 2.5 to 6 meters was rather good. Thus, it was possible to see and collect many young snails and egg masses at those depths. Since such observations have been duplicated in other parts of the lake for *H. campanulatum smithi*, *L. emarginata angulata* and *P. sayii crassa*, it does not seem unlikely that many of these snails complete their entire life cycles and reproduce normally without coming to the surface. Such behavior is very similar to that exhibited by abyssal pulmonates. In Douglas Lake, a few representatives of *P. parkeri* pass the entire summer naturally submerged. However, such instances occur much less frequently in this species than in *H. antrosom percarinatum*, *H. campanulatum smithi*, *P. sayii crassa*, and *L. emarginata angulata*. A large *L. stagnalis appressa* was collected August 2, 1932, in water approximately 7.5 meters deep. The head of the snail was directed shoreward. It was the only specimen of this species collected on Douglas Lake in water over 1.5 meters deep during the late summer and early fall months. *P. parkeri* was taken several times in water 3.5 to 4.5 meters deep in company with *L. emarginata angulata*, *P. sayii crassa*, *H. antrosom percarinatum*, and *H. campanulatum smithi*. *H. trivolvis* is one of the earliest of the 7 lake species to come to the surface in the spring, and it remains in very shallow water throughout the entire summer and early fall. A thriving aggregation of *L. stagnalis sanctaemariae* was discovered at Copper Harbor, Upper Peninsula, Michigan, September 3, 1932, clinging to rocks in water having a temperature of 19.5°C. and a depth of approximately 20 to 25 centimeters. All specimens examined had their lung chambers

filled with water indicating that, in all probability, these snails had lived the entire summer in shallow water without coming to the surface.

Following a period of cold weather in the fall of sufficient duration to lower the temperature of lake water from 20°C. to less than 10°C. there is a definite change in the orientation of the bodies of snails from that in which the head is directed shoreward to that in which the head is directed towards the deeper water. This orientation is followed by a very gradual migration which is similar to the early summer migration from deep to shallow water in that certain species precede others.

During the latter part of November, 1931, a trip was made from Ann Arbor to Douglas Lake to determine the approximate distribution of lake pulmonates at that time of year. The temperature of the water was 5.5°C. Examinations were made at the Ingleside and Hook Point habitats. Table 13 gives the approximate distribution of six species of snails at that time of year.

TABLE 13

APPROXIMATE MAXIMUM DISTRIBUTION OF LAKE PULMONATES AT THE INGLESIDE AND HOOK POINT HABITATS, NOV. 22, 1931
(TEMPERATURE OF WATER, 5.5°C.)

Habitat	Species	Approximate depth of max distribution in meters.
Ingleside	<i>L. stagnalis appressa</i>	0.7
	<i>H. trivolvis</i>	0.5
	<i>P. parkeri</i>	1.0
Hook Point	<i>H. antrosom percarinatum</i>	More than 1.0
	<i>H. campanulatum smithi</i>	" " 1.0
	<i>L. emarginata angulata</i>	" " 1.0

Due to the fact that at Hook Point the majority of the snails had migrated into water too deep for wading with hip boots, it was impossible to determine the maximum distribution at this habitat. The relation of slope to the distribution of snails in the Ingleside and Hook Point habitats is discussed elsewhere (pp. 379–383). It is interesting to note (table 13) that the migration of *P. parkeri* is in advance of both *L. stagnalis appressa* and *H. trivolvis*. Perhaps this advanced position in the migration may be correlated with the amount of oxygen consumed by the different species, those species absorbing less oxygen per gram weight of soft parts per hour being better equipped physiologically to begin their migration into the deeper water at an earlier date than are those snails with a higher oxygen consumption. *L. stagnalis appressa* and *H. trivolvis* may be retarded in their migration until the temperature of the water is low enough so that oxygen sufficient for their reduced physiological needs may be extracted directly from the water. Data from the results of submergence (pp. 370–377) and

oxygen consumption (pp. 365-370) experiments make such a postulation entirely plausible.

A colony of *L. columella* kept under observation in a small lake near Ann Arbor, Michigan, all migrated from the surface to depths ranging from 0.7 to 1.5 meters when the temperature of the water was lowered from 12.8° to 3.5°C. Although ordinarily considered a surface species, representatives of *L. columella* remained in these depths through the entire winter and early spring months.

During the winter months when most northern lakes are covered with ice, those snails that are not frozen fast in the shallow littoral regions pass a more or less inactive life in the open, deeper water. The sluggish activity of snails under ice has been observed during the winter in pools and small lakes near Ann Arbor, Michigan. Among the species seen to crawl slowly about under a thin coating of ice are *H. trivolvis*, *L. columella*, *P. sayii*, *P. gyrina*, and *Gryaulus deflectus*. Cook (1895) has recorded instances of *Lymnaea* crawling about on the under surface of ice. Undoubtedly, all fresh-water pulmonates move about more or less during the winter months providing they are in the open water. Apparently, but few observations have been made on snail life during the winter. Certainly from the observations just cited, metabolism is not always lowered to such an extent that movements entirely cease during the winter months.

After the ice breaks up in the spring and the temperature of the water is raised to 10°-16°C., due to several consecutive days of warm weather, the stimulus provided by the higher temperature causes the migration from the deeper water to the surface. This is especially true for snails, such as *L. palustris*, *L. exilis*, *P. sayii*, *H. trivolvis*, and *L. columella*, that inhabit the shallow pools and smaller lakes. In the spring of 1932, several *L. columella*, *L. palustris* and *L. exilis* were observed at the surface of a woodland pool the water of which was 10.5°C. These snails were beginning their reproductive cycle since several were found in the act of copulation and a few freshly deposited egg masses were collected. From many observations made in spring on the lakes and pools in the vicinity of Ann Arbor, Michigan, it appears that by the time the water has acquired a temperature of 13°-16°C. many of the snails occurring in such situations are on the surface or clinging to objects just beneath it. Unfortunately, observations have not been made on the beginning of the spring migration of snails in larger lakes. Hence, the spring temperatures which serve to stimulate snail life of the deeper regions to migrate toward the shallow, littoral zone are not known.

Relation to slope.—The importance of the general shape of the shelf in determining to a large extent the dispersion of snails is clearly evidenced by comparing the distribution of *H. antrosom percarinatum* at the Grapevine and Hook Point habitats (fig. 23; fig. 25). As described (p. 379), these

regions present distinct contrast, and serve as excellent habitats for the study of distribution as influenced by type of shoal.

At Grapevine Point, the maximum population of *H. antrosom percarinatum* occurred at a depth of 3 meters, whereas, at Hook Point, the maximum number of this species was found at 0.6 meters depth. Due to the very narrow shelf at Hook Point and the rather sharp decline of the shelf into deep water, snails do not have to migrate more than 9 meters from the shoreline into the lake until they are in water 2.5 meters deep (fig. 25). This relatively short migration brings them into water which is deep enough to insure protection from the ice-blocked zone in the late fall, winter, and spring months. In direct contrast to this habitat, those snails which migrate into shallow water at Grapevine Point during the summer months must, in the fall, migrate at least 30 meters in order to reach a protected zone (fig. 23). However, as indicated in fig. 23, *H. antrosom percarinatum* and *P. sayii crassa* move out into the lake for a distance of more than 90 meters from the shore line into water more than 5.5 meters in depth. Both species are very sluggish in movements, and as mentioned (p. 384), undoubtedly many never complete their migration. The chances for completion of the migratory cycle of any snail are much greater on a narrow shelf dropping rather abruptly into deep water, than on a very wide, gently sloping shelf on which the snail must move for a considerable distance in order to emerge from the protected zone to the surface. An example of the latter type of habitat is found at Ingleside (fig. 27).

Although the species of snails given in table 13 are different in the two habitats, nevertheless, the approximate distribution from the standpoint of depth of the six species (three at Hook Point and three at Ingleside) is so different that the slope of the shelf must be taken into consideration in attempting an explanation of this distribution. It has been observed that snails in the Hook Point habitat are the first to appear in the early summer and the first to disappear into the deeper waters in the late fall. Obviously, as long as the same species are concerned, the difference in time of emergence in the spring, and natural submergence in the fall is largely due to the migration distances that snails must cover in order to reach deeper water in the late fall or shallow water in the late spring or early summer. This migration distance is much more significant in these species whose oxygen consumption is relatively high than in those species with a much lower oxygen consumption. For example, such species as *H. antrosom percarinatum*, *P. sayii crassa* and *H. campanulatum smithi*, are not necessarily handicapped by a failure to complete their migration due to the retarding influence of a wide shelf, for they can easily tide over the summer and fall months in shallow water without emerging to the surface. However, such snails as *L. stagnalis appressa* and *H. trivolvis* are handicapped by this situation due to their increased need for oxygen as the water warms during

early summer. The large number of empty shells washed ashore during the summer in the Ingleside habitat compared to the smaller number of shells from the same species at Hook Point may be partly accounted for as follows: Snails in a habitat which requires a long migration in order for them to over-winter in a protected zone and come to the surface relatively early in the spring for additional air to meet their increased oxygen demands, have a greater morality than do snail inhabiting a narrow shelf. Their time of travel is prolonged, due to the greater migration distance, and cutaneous respiration alone is not always adequate to sustain life in the warmer water. Hence, in such a habitat, this higher mortality is evidenced by the number of shells washed ashore.

HIBERNATION

In nature.—Hibernation as defined by Pycraft (1929) is "the more or less comatose condition in which certain animals pass the winter in cold latitudes." This definition when applied in its broadest sense (*more or less* comatose condition) may include the activities of fresh-water pulmonates during the winter months when the streams and lakes are frozen over. It is true that aquatic snails become lethargic in their movements at low temperatures, yet, as pointed out (p. 386), they remain more or less active throughout the winter months as long as there is open water in which to move about. A state of total inactivity during this period is probably brought about only by mechanical means, such as being frozen fast in ice. Many observations have been made by the writer on snails that were active in open water, the surface of which was covered by a layer of ice. These snail activities are continued until the entire mass of water is frozen solid and the animals are embedded within the ice.

The ability of snails to endure extremely low temperatures for prolonged periods is recorded in the literature by several writers. *Aplexa hypnorum*, a very fragile fresh-water pulmonate has been found (Cook, 1895) "on the peninsula of Taimyr, North Siberia, in 73 30 N. lat., a region whose mean annual temperature is below 10°F. with a range of from 40°F. in July to -30°F. in January." Granier (1840) records *Limnaea auricularia* frozen solid in a mass of ice and reviving after being thawed out. Professor Earl C. O'Roke of the University of Michigan informs the writer that he has found *L. palustris* frozen fast in ice in a pool near Laramie, Wyoming, and that after the snails were thawed out, all were found to be alive.

In many small streams, the pulmonate snail fauna is quite plentiful. Snails inhabiting such situations must be able to meet the exigencies of their environment in order to survive. In the northern parts of the United States, many streams freeze solid during the winter months. As pointed out (p. 381), when the water is cooled down to a rather low temperature this

change is usually accompanied by a migration of snails from the surface to the bottom of the pool which they are inhabiting. Consequently, most snails that inhabit the smaller streams react in this way to a low temperature in the autumn. As the water gradually freezes on the surface and the layer of ice becomes thicker, snails may burrow down into the soft muck or vegetation in the stream bed and overwinter in such situations. However, if the stream freezes solid, the snails become surrounded by the frozen materials in which they have burrowed. The writer has dug blocks of ice from several small streams in Kansas and Michigan, and if snails were present they were almost invariably frozen solid in the muck and vegetation of the stream bed rather than in the clear ice near the surface. The ability of the smaller pulmonates to overwinter under such conditions is proved by the abundance of adult snails in the smaller streams when the ice first melts in the spring. It is true that many of the snails die during the winter. The high mortality during this time may be partly due to a weakened resistance to such adverse conditions brought on by old age or parasitism. In order to determine the condition of snails frozen solid in roadside pools and the smaller streams near Ann Arbor, Michigan, blocks of ice were dug from such situations, the frozen material melted, and the snails were then placed in an aquarium filled with water at room temperature, and, if they showed signs of life within a period of two days, were regarded as living. Due to the mild weather of 1931 and 1932, data could not be obtained on the condition of snails frozen solid in their natural environment for a period longer than approximately two weeks.

TABLE 14

NUMBER OF SNAILS LIVING AND DEAD RECOVERED FROM ICE AFTER BEING FROZEN SOLID FOR APPROXIMATELY TWO WEEKS

Species	No. living	No. dead	Per cent living
<i>Physa gyrina</i>	18	11	62
<i>Gyraulus deflectus</i>	46	10	82
<i>Lymnaea obrussa</i>	38	6	86
<i>Helisoma trivolvis</i>	8	2	80

The data presented in table 14 show that most individuals of all four species are able to survive at least for a two weeks period when frozen solid in ice. In liberating the snails from the ice, it was observed that most of the dead snails were those frozen solid in clear ice rather than frozen into the bottom materials. It may be that a snail under such conditions has a much better chance of survival if it is frozen into materials that form air spaces in the ice rather than being enveloped completely within solid ice. Due to the extremely low temperature in such surroundings, the oxygen consumption of the snails is reduced to an extent that the air present in those spaces may be very helpful in enabling the animal to tide over prolonged periods

of freezing. Since most snails living in shallow water burrow into the muck and vegetation during low temperatures in the fall, winter, or early spring, the probability is that such behavior may decrease considerably the mortality that would otherwise occur if they were frozen solid in clear ice.

Experiments.—In all probability, many lake pulmonates that fail to migrate from the shallow, littoral zone into the deeper water of the lake are frozen solidly in ice during the cold months of the year. No winter observations were made on the snails inhabiting Douglas Lake, and at the present time it is impossible to present figures on the approximate per cent of snails that fail to complete their migration to the deeper water in the fall. However, a large number of representatives of all nine species of snails collected in the Douglas Lake region were transported to the zoology laboratory at the University of Michigan during the early fall of 1931 and were available for experimental work. In order to determine whether or not lake pulmonates reared in aquaria for a period of one and one-half months could survive if frozen abruptly or gradually in a solid cake of ice, the following experiment was performed.

One group of snails of the upper size range (table 3) consisting of specimens of all nine species was transferred directly from an aquarium containing water at room temperature ($25.5^{\circ}\text{C}.$) to the freezing pans of an electric refrigerator. They were then frozen in solid cakes of ice within a period of 12 hours. A second group of snails containing specimens of all nine species was transplanted from an aquarium filled with water at room temperature ($25.5^{\circ}\text{C}.$) to another aquarium in an open room where the temperature was decidedly lower. After remaining in this room for two days, the aquarium containing the snails was then transferred to the refrigerator and the water cooled down to $3.5^{\circ}\text{C}.$ during a period of 36 hours. Thus the snails of this second group were allowed a period of 84 hours to become acclimated to the low temperature before being frozen. After this preparation period, they were then frozen in the same way as group one. At the termination of this 12-hour period of freezing, the cubes of ice containing the snails were removed from the freezing pans and placed in water at room temperature where they were allowed to thaw. If a snail exhibited signs of activity within a period of 24 hours after it had been liberated from the ice, it was regarded as living. The results of this experiment are given in table 15.

The data in table 15 show that the per cent surviving is nearly twelve times greater in the group subjected to a gradual change than in the group subjected to an abrupt change of temperature. The question then arose as to how long snails could live experimentally frozen in cakes of ice. The following experiment was performed.

Snails of three species (due to lack of material only three species were used) were subjected to gradual cooling as described in the preceding ex-

TABLE 15

NUMBER OF SNAILS SURVIVED FREEZING WHEN SUBJECTED TO ABRUPT AND TO GRADUAL TEMPERATURE CHANGE

Species	Condition of temp. change					
	Abrupt change			Gradual change		
	No. snails	No. surv.	Per cent surv.	No. snails	No. surv.	Per cent surv.
<i>L. megasoma</i>	6	0	0.0	6	2	33.3
<i>L. stagnalis appressa</i>	14	0	0.0	14	5	35.7
<i>L. palustris</i>	10	1	10.0	10	6	60.0
<i>L. emarginata angulata</i>	16	1	6.2	16	8	50.0
<i>P. parkeri</i>	8	0	0.0	8	3	37.5
<i>P. sayii crassa</i>	20	1	5.0	20	8	40.0
<i>H. trivolvis</i>	12	2	16.6	12	8	66.6
<i>H. campanulatum smithi</i>	10	0	0.0	10	5	50.0
<i>H. antrosom percarinatum</i>	10	0	0.0	10	4	40.0
Average per cent survived			4.2			45.9

periment, and frozen solid in ice cubes. Every two days for a period of 16 days, ice cubes containing specimens of each of the three species were thawed out and the snails recovered. The results of this experiment are given in table 16.

TABLE 16

NUMBER OF SNAILS SURVIVING DEFINITE PERIODS OF FREEZING

Species	No. in ice cube	Number living						
		2nd day	4th day	6th day	8th day	10th day	12th day	14th day
<i>L. emarginata angulata</i>	3	1	2	1	0	2	1	0
<i>P. sayii crassa</i>	3	0	1	0	1	0	0	0
<i>H. trivolvis</i>	3	2	3	2	2	1	0	1

From this experiment (table 16), it is seen that *H. trivolvis* can survive when frozen solid in ice for a period of at least 14 days. *P. sayii crassa* is able to survive such conditions for a period of at least 8 days, and *L. emarginata angulata* 12 days. Just how much longer snails of the species *H. trivolvis* can endure such conditions is not known.

AESTIVATION

In nature.—It has long been known that many of the smaller species of aquatic pulmonates, such as *L. obrussa*, *L. humilis modicella*, and *Gyraulus parvus*, spend a great share of their time out of water, and when placed in an aquarium many crawl up the sides and even remain out of water until they die, apparently making no effort to crawl back into the water. Pilsbry (1896) reports the case of *L. bulimoides cockerelli* being out of water for a

period of 45 days and, when placed in water, approximately 50 per cent had survived the exposure. Such a hardy species as *L. peregra* has been found (Cooke, 1895) buried to a depth of three inches in mud, and *L. truncatula* has been uncovered (Jeffery, 1882), in hard mud at a depth of eighteen inches. Mozley (1932) cites *L. palustris* inhabiting a pond which dries up to such an extent that the snail is active and feeds only two months out of every twelve. Mr. Calvin Goodrich, University of Michigan Museum informs the writer that he found *L. stagnalis* alive in dried cakes of mud in Ottawa Lake, Monroe Co., Michigan. Henderson (1932) reports *L. bulimoides cockerelli* alive and of normal size in a pool that seldom contains water for more than sixty days in a year, and during 1931 was occupied by water for less than thirty days. There are also many other instances on record of pulmonate snails successfully surviving prolonged periods of drouth in their natural environment as well as being artificially removed from water for an extended length of time. However, practically all records pertain only to those snails that inhabit swampy regions and pools. Clessin (1880) stated that *Lymnaea* is able to live for a considerable time in moist air but doubted very seriously the possibility of accustoming them to this condition.

In collecting a large series of *L. stagnalis* and *L. palustris* in a swamp adjoining Black Lake and Black River in Cheboygan County, Michigan, an excellent opportunity was afforded the writer to study the habits of these snails when they are forced to burrow in muck and vegetation in order to survive conditions of drouth. In a few areas in this locality, no snails were visible at the surface but upon digging into beds of *Elodea* and *Myriophyllum*, many living snails were found. Most of the snails that were completely exposed, however, were dead. In such a habitat, it would be of vital importance for the snail to burrow into the vegetation in order to escape the drouth since many of these areas had dried up to such an extent that a hard, dry crust was formed on the surface of the muck. Upon breaking this covering, many living snails of the species mentioned were found. Some had burrowed to depths of 10-14 centimeters, living in vegetation that was saturated with water; others were situated just below the surface and instead of their bodies being partly extruded as was the case of those found deeper in the vegetation, they were drawn far back into the shells. In a few instances, an epiphragm consisting of hardened mucus was formed over the aperture. Such a structure, according to Cooke (1895), is produced by only a very few of the fresh-water snails. However, a few such structures have been observed in representatives of each of the nine species of snails used in this work. These were formed by the snails during natural aestivation or aestivation produced experimentally. The epiphragm undoubtedly functions as it does in land snails, namely, to prevent the rapid evaporation of moisture from the body. Along the shores of Douglas Lake, many living

snails have been collected in the early fall from pools that were dry and had dry crusts formed over their surfaces. Aestivation, then, is a natural response of most fresh-water snails living in temporary pools, and streams, and this phenomenon aids the snails in tiding over prolonged periods of drouth.

Experiments.—The fresh-water lake pulmonates seldom have need for resorting to aestivation during the summer unless the shallows containing them dry up completely or are cut off from the lake proper by the formation of sand bars with subsequent complete evaporation. Under such adverse conditions, they are able to endure rather long periods of gradual desiccation. The duration of their existence under such circumstances can be shortened, however, by subjecting living animals to abrupt exposure to drouth. This is much more severe than the normal process of drying as it occurs in nature.

An experiment was conducted to determine whether the Douglas Lake pulmonates could survive prolonged drouth in an artificial habitat as well as in a natural one. A rectangular area, 1×2 meters was boxed off with lumber and this enclosure filled with muck collected from a protected region at Hook Point. The site for the experiment was selected in a shady place where the snails were never exposed to direct sunlight. All of the different specimens used in the experiment were subjected to drying in this area. Some were buried to a depth of three centimeters in the muck and others placed on the surface. This plot was kept moist by sprinkling lake water over the muck at intervals of 2–3 days. The snails were kept under observation from July 3, to Sept. 10. At the close of that period, all of the snails were recovered, the dead ones separated from the living, and the data recorded. The results are given in table 17.

TABLE 17

SNAILS SUBJECTED FOR 68 DAYS TO CONDITIONS OF DESICCATION PRODUCED EXPERIMENTALLY

Species	No. of snails	Remarks	Living or dead at end of exp.
<i>L. stagnalis appressa</i>	23	Buried	1 living
<i>L. emarginata angulata</i>	18	"	4 "
<i>L. megasoma</i>	12	"	1 "
<i>L. palustris</i>	38	"	8 "
<i>P. parkeri</i>	31	"	dead
<i>P. sayii crassa</i>	24	"	3 living
<i>H. trivolvis</i>	20	"	8 "
<i>H. campanulatum smithi</i>	22	"	1 "
<i>H. antrosom percarinatum</i>	18	"	dead
Equal no. of specimens of each species	72	Snails on surface	dead

The resistance to desiccation (table 17) is greater in snails that are forced to undergo such natural phenomena more frequently than do the

lake pulmonates. This is best exemplified in *L. palustris* and *H. trivolvis*. All snails placed on the surface and exposed directly to the air failed to survive the duration of the experiment. Most of them died within a period of twenty days after the beginning of the experiment. The typical lake pulmonates, however, were the first to die, the marsh species surviving a longer period of exposure.

Specimens representing the 9 species were placed on the surface of a beach pool near Hook Point, July 8, 1932. The bottom of the pool was covered with a watery ooze approximately 2 centimeters deep. During the course of the experiment, the standing water completely evaporated and a thin, dry crust formed over the surface of the muck. On Sept. 9, these snails were recovered and those showing signs of life were placed in aquaria. The data derived from this experiment are given in table 18.

TABLE 18
SNAILS SUBJECTED TO NATURAL CONDITIONS OF DESICCATION FOR 62 DAYS

Species	No. of snails	No. alive at end of exp.
<i>L. stagnalis appressa</i>	16	5
<i>L. emarginata angulata</i>	20	6
<i>L. megasoma</i>	10	4
<i>L. palustris</i>	50	28
<i>P. parkeri</i>	20	3
<i>P. sayii crassa</i>	22 (15 recovered)	4
<i>H. trivolvis</i>	15	8
<i>H. campanulatum smithi</i>	18 (16 recovered)	4
<i>H. antrosom percarinalum</i>	18 (12 recovered)	6

Although the snails were placed on the surface of the pool at the beginning of the experiment, it was found when they were recovered, that practically all of them had burrowed into muck from depths of 1-7 centimeters. Since the conditions to which these snails were subjected were natural, the assumption is that in other similar environments the mortality of these species would be approximately the same as in the habitat described. In comparing the data in tables 17 and 18, it will be seen that although the survival is higher for all species, in the natural beach pool nevertheless, the resistance to such conditions was approximately the same in all specimens of the same species. The data show that lake pulmonates of the species used in this work may, under adverse conditions of prolonged drouth, survive for periods as long as 62 days without recourse to the open water.

SUMMARY

1. Investigations have been made on the respiration and annual migratory cycle in nine species of aquatic pulmonate snails.
2. A definite correlation appears to exist between the capacity of the pulmonary sac and the weight of the snail. However, the capacity of the

pulmonary sac in smaller snails appears to be much greater in proportion to their weight than in the larger snails.

3. In vegetation areas, snails make their ascent to the surface by flotation or by traveling over submerged objects. In exposed areas, snails reach the surface by migrating shoreward until they are in water shallow enough to accomplish the surface breathing act.

4. A definite relationship exists between the amount of air inspired and the period of inspiration, namely, the longer this period the greater the amount of air inspired.

5. The average interval between breathing periods varies in all nine species. It is much shorter in the swamp or marsh species than in most of the seven lake pulmonates.

6. Temperature plays an important part in determining the interval between breathing periods. In water at low temperature ($11^{\circ}\text{C}.$), the average interval between breathing periods for the 9 species is nearly 22 times as long as in water at $21^{\circ}\text{C}.$

7. The oxygen content also determines, to a large extent, the interval between breathing periods. The average interval between breathing periods for the nine species in water with an oxygen content of 6.4 cc. per liter, is approximately 3 times as long as in water with an oxygen content of 1.7 cc. per liter.

8. The amount of oxygen consumed per gram weight of soft parts per hour is different for each of the nine species. The marsh species and the species inhabiting protected regions consume much more oxygen than those inhabiting exposed areas.

9. Snails having shorter intervals between breathing periods consume more oxygen than do those with longer periods between breathing.

10. The oxygen consumption of each of the nine species is much less at a low temperature ($5.5^{\circ}\text{C}.$) than at room temperatures (14.5° – $32^{\circ}\text{C}.$).

11. A greater number of snails with air present in the pulmonary chamber survived prolonged submergence than did those whose pulmonary chambers had been previously deflated.

12. The total number of snails surviving 62 days of experimental submergence was more than 3 times as great in water at $11^{\circ}\text{C}.$, than in water with a temperature of 21.6° – $25.5^{\circ}\text{C}.$

13. In submergence experiments, the mortality among those species whose oxygen consumption is the highest was much greater than among those with a lower oxygen consumption.

14. Some individuals of each of the nine species represented withstood direct submergence for periods as long as 62 days in the lower temperatures. All snails that were alive at the termination of 62 days of experimental submergence had their pulmonary sacs filled with air.

15. When the temperature of the water declines from 21° to 10°C., snails of those species of *Lymnaea*, *Helisoma*, and *Physa* used in the experiments migrated from the surface to deeper water. A change of temperature in the opposite direction (10° to 21°C.) is accompanied by an ascent from the deeper water to the surface.

16. In all probability, many individuals of the species *H. campanulatum smithi*, *H. antrosom percarinatum*, *L. emarginata angulata*, and *P. sayii crassa*, complete their life cycles and reproduce normally without emerging for air.

17. All snails collected in the deep water of Douglas Lake had their pulmonary sacs filled with water. Evidently the pulmonary sac functions as a gill.

18. All seven species of Douglas Lake pulmonates manifest regular seasonal migrations. During the fall months when the temperature of the water declines, most of the individuals migrate from the shallow, littoral zone to the deeper water where they overwinter. When the water warms up in the late spring and early summer, these same snails move from the deeper water shoreward.

19. Snails inhabiting a narrow shelf disappear into the deeper water adjoining the shelf earlier in the autumn and appear earlier in the spring than do those inhabiting a gradually sloping shelf. This is apparently due to the much shorter migration distance of the narrow shelf.

20. Representatives of all nine species withstood experimental freezing in cakes of ice when allowed a period of 84 hours to become acclimated to the low temperature before being frozen.

21. All seven species of lake pulmonates may, under adverse conditions of prolonged drouth, survive for periods as long as 62 days without recourse to open water.

22. The resistance to desiccation is greater in snails that are forced to undergo in nature such phenomena more frequently than in the lake pulmonates.

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TABLE 19
INTERVALS BETWEEN BREATHING PERIODS OF *L. megasoma*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	0	0	3	0	3	0	3	4	2	0	1	2	18	540	360.0	11.0-11.0	5.2
	1	4	2	0	3	6	2	7	0	5	8	1	39	495	152.3	12.5-16.8	6.4
	9	6	9	24	12	15	8	7	7	18	16	13	144	375	31.2	12.8-20.0	1.7-2.6
	10	9	12	24	8	12	8	10	16	18	14	11	162	552	40.8	21.0-21.0	6.1
{	15	21	22	17	18	15	17	10	14	9	6	31	195	375	23.0	28.8-24.4	3.6-4.1
													Average	121.4			

TABLE 20
INTERVALS BETWEEN BREATHING PERIODS OF *L. emarginata angulata*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	0	0	0	0	3	0	0	0	2	0	1	0	6	540	1080.0	11.0-11.0	5.2
	6	3	0	0	3	0	6	0	4	0	1	0	23	495	236.9	12.5-16.8	6.4
	3	2	0	9	5	2	7	0	3	2	0	3	36	375	125.0	12.8-20.0	1.7-2.6
	9	1	9	6	0	3	3	4	2	1	2	0	40	552	165.6	21.0-21.0	6.1
{	3	38	17	15	25	16	10	12	32	29	6	99	212	375	21.2	28.8-24.4	3.6-4.1
													Average	325.7			

TABLE 21
INTERVALS BETWEEN BREATHING PERIODS OF *L. palustris*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	1	6	0	6	9	0	3	6	0	4	2	1	38	540	170.5	11.0-11.0	5.2
	6	12	9	9	30	8	7	24	16	0	7	10	138	495	43.0	12.5-16.8	6.4
	4	15	12	18	51	28	17	11	8	23	31	13	231	375	19.4	12.8-20.0	1.7-2.6
	15	10	18	45	69	39	52	29	18	57	41	12	415	552	15.9	21.0-21.0	6.1
{	16	6	21	30	23	18	36	32	27	19	45	51	324	375	13.8	28.8-24.4	3.6-4.1
													Average	52.5			

TABLE 22
INTERVALS BETWEEN BREATHING PERIODS OF *H. trivialis*

	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
Number of times seen to breathe	0	0	3	0	0	0	3	0	1	2	0	1	10	540	648.0	11.0-11.0	5.2
	18	0	3	0	3	2	1	0	1	6	0	0	34	495	174.7	12.5-16.8	6.4
	3	6	0	3	4	7	3	2	5	1	0	4	38	375	118.4	12.8-20.0	1.7-2.6
	9	15	9	3	12	14	10	8	6	3	0	7	96	552	69.0	21.0-21.0	6.1
	2	8	19	8	7	12	4	4	6	6	12	10	98	375	45.9	28.8-24.4	3.6-4.1
Average													211.2				

TABLE 23
INTERVALS BETWEEN BREATHING PERIODS OF *P. sayii crassa*

	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
Number of times seen to breathe	0	0	0	0	0	0	0	0	0	0	0	1	1	540	6480.0	11.0-11.0	5.2
	0	1	0	3	0	0	2	0	0	2	0	1	9	495	660.0	12.5-16.8	6.4
	12	1	3	3	4	0	2	3	0	1	0	2	31	375	144.8	12.8-20.0	1.7-2.6
	6	6	18	1	27	6	0	4	8	10	22	14	46	552	143.5	21.0-21.0	6.1
	4	5	3	9	6	10	1	2	3	2	0	1	122	375	36.8	28.8-24.4	3.6-4.1
Average													1493.0				

TABLE 24
INTERVALS BETWEEN BREATHING PERIODS OF *P. parkeri*

	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
Number of times seen to breathe	0	1	0	0	0	2	0	0	2	0	0	1	6	540	1080.0	11.0-11.0	5.2
	1	2	8	2	0	3	1	4	0	2	1	0	24	495	247.5	12.5-16.8	6.4
	2	3	6	4	2	8	7	4	6	7	3	5	57	375	78.9	12.8-20.0	1.7-2.6
	9	9	3	6	5	0	4	10	3	8	9	1	67	552	98.8	21.0-21.0	6.1
	33	15	6	45	21	6	5	29	38	16	7	10	231	375	19.4	28.8-24.4	3.6-4.1
Average													304.9				

TABLE 25
INTERVALS BETWEEN BREATHING PERIODS OF *H. campanulatum smithi*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	0	1	0	0	0	0	0	0	0	0	0	0	1	540	6480.0	11.0-11.0	5.2
	3	3	3	6	0	3	1	2	4	0	1	6	32	495	185.6	12.5-16.8	6.4
	2	0	8	7	9	6	3	2	5	8	10	11	71	375	63.3	12.8-20.0	1.7-2.6
	5	1	3	4	6	9	0	2	0	1	2	7	40	552	165.5	21.0-21.0	6.1
	3	6	6	15	9	2	7	5	8	15	16	4	96	375	46.8	28.8-24.4	3.6-4.1

Average 1388.2

TABLE 26
INTERVALS BETWEEN BREATHING PERIODS OF *H. antrosom percarinatum*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	0	1	0	2	0	0	0	0	0	0	0	0	3	540	2160.0	11.0-11.0	5.2
	3	4	7	2	1	4	0	0	2	5	1	3	32	495	185.6	12.5-16.8	6.4
	3	0	7	5	9	12	5	6	9	11	10	6	83	375	54.2	12.8-20.0	1.7-2.6
	3	4	3	9	6	7	0	0	4	7	2	0	45	552	124.9	21.0-21.0	6.1
	14	11	17	9	6	3	1	12	9	12	2	4	100	375	45.0	28.8-24.4	3.6-4.1

Average 513.9

TABLE 27
INTERVALS BETWEEN BREATHING PERIODS OF *L. stagnalis appressa*

Number of times seen to breathe	Specimen number												Total no. times seen to breathe	Duration of exp. in min.	Avg. interval in min.	Temp. in degrees C.	Oxygen in c.c. per l.
	1	2	3	4	5	6	7	8	9	10	11	12					
{	3	6	3	0	1	2	6	0	2	3	1	3	30	540	216.0	11.0-11.0	5.2
	9	12	12	2	24	18	9	0	15	3	6	24	134	495	44.3	12.5-16.8	6.4
	21	42	18	12	27	30	15	30	40	48	54	48	385	375	11.6	12.8-20.0	1.7-2.6
	9	6	3	33	24	12	39	6	18	27	24	12	213	552	31.0	21.0-21.0	6.1
	75	18	27	51	42	33	39	42	24	15	60	21	447	375	10.0	28.8-24.4	3.6-4.1

Average 62.6

TABLE 28
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *L. palustris*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
12.64	18 hrs. 10 min.	15.0-29.5	9.24	0.04023
11.46	17 " 50 "	16.6-31.0	7.77	0.03801
13.92	21 " 15 "	15.2-30.5	10.22	0.03454
21.17	10 " 30 "	16.6-31.0	7.70	0.03463
22.38	10 " 50 "	14.5-30.0	8.82	0.03637
17.29	12 " 00 "	14.5-30.0	7.98	0.03846
16.14	14 " 40 "	14.5-30.0	8.68	0.03665
10.07	13 " 45 "	16.0-29.5	7.07	0.05105
			Average	0.03874
9.68	26 hrs. 15 min.	5.5	3.12	0.01227
10.09	25 " 20 "	5.5	2.56	0.01001
11.74	26 " 10 "	5.5	2.84	0.00926
12.36	24 " 8 "	5.5	3.92	0.01313
14.16	24 " 35 "	5.5	4.16	0.01194
8.91	23 " 18 "	5.5	1.92	0.00924
10.49	25 " 40 "	5.5	2.80	0.01039
11.61	18 " 35 "	5.5	2.36	0.01093
			Average	0.01090

TABLE 29
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *P. parkeri*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
14.17	26 hrs. 30 min.	14.5-28.0	3.87	0.01030
21.08	19 " 10 "	15.5-30.5	3.06	0.00757
10.52	11 " 32 "	21.0-28.0	3.34	0.01928
23.91	8 " 30 "	22.0-30.5	3.45	0.01697
18.17	23 " 00 "	20.0-32.0	3.27	0.00782
16.84	15 " 10 "	24.5-30.0	3.27	0.01280
22.17	30 " 30 "	16.0-31.5	6.24	0.00922
			Average	0.01199
15.14	25 hrs. 25 min.	5.5	1.62	0.00421
23.02	24 " 40 "	5.5	2.67	0.00470
11.17	21 " 55 "	5.5	1.74	0.00710
10.86	21 " 10 "	5.5	2.13	0.00926
9.38	23 " 23 "	5.5	1.20	0.00548
21.18	25 " 10 "	5.5	3.00	0.00562
19.20	26 " 00 "	5.5	1.11	0.00222
			Average	0.00551

TABLE 30
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *P. sayii crassa*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
3.83	18 hrs. 15 min.	19.5-25.5	0.40	0.00572
4.67	19 " 30 "	19.0-25.5	0.58	0.00636
3.79	17 " 45 "	21.0-28.0	0.36	0.00535
			Average	0.00581
2.86	24 hrs. 00 min.	5.5	0.07	0.00010
5.62	23 " 10 "	5.5	0.13	0.00099
3.38	25 " 8 "	5.5	0.11	0.00129
			Average	0.00079

TABLE 31
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *L. emarginata angulata*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in cc. per gm. wt. per hr.
11.16	26 hrs. 25 min.	14.5-28.0	2.55	0.00864
15.06	18 " 45 "	15.5-30.5	2.45	0.00867
13.28	11 " 30 "	21.0-28.0	0.75	0.00491
15.31	11 " 25 "	22.0-30.5	1.15	0.00658
17.25	10 " 30 "	20.0-32.0	1.30	0.00717
16.18	8 " 00 "	24.5-30.0	2.45	0.01892
19.11	9 " 45 "	16.0-31.5	2.60	0.01395
11.57	23 " 15 "	14.5-25.3	3.35	0.01244
10.93	17 " 10 "	24.0-25.3	2.19	0.01166
14.62	18 " 14 "	23.0-29.0	2.60	0.00975
			Average	0.01141
18.21	19 hrs. 30 min.	5.5	1.83	0.00515
13.42	19 " 35 "	5.5	1.44	0.00547
10.68	23 " 16 "	5.5	0.57	0.00229
11.23	32 " 00 "	5.5	0.75	0.00208
10.32	24 " 30 "	5.5	0.54	0.00213
17.19	23 " 10 "	5.5	1.26	0.00316
16.24	18 " 30 "	5.5	1.20	0.00399
18.19	26 " 45 "	5.5	2.07	0.00425
21.17	24 " 30 "	5.5	1.74	0.00335
			Average	0.00354

TABLE 32

DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *H. campanulatum smithi*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
6.92	15 hrs. 10 min.	14.5-28.0	0.57	0.00542
4.89	14 " 40 "	15.5-30.5	0.54	0.00772
10.36	12 " 50 "	21.0-28.0	1.53	0.01150
11.72	15 " 30 "	22.0-30.5	2.07	0.01139
9.83	17 " 25 "	20.0-32.0	2.04	0.01191
8.67	16 " 10 "	24.5-30.0	1.47	0.01048
			Average	0.00973
5.87	26 hrs. 20 min.	5.5	0.36	0.00232
6.88	26 " 10 "	5.5	0.52	0.00288
7.49	26 " 10 "	5.5	0.68	0.00346
10.23	23 " 20 "	5.5	0.92	0.00385
11.09	23 " 40 "	5.5	0.84	0.00319
9.75	36 " 10 "	5.5	1.16	0.00328
			Average	0.00314

TABLE 33

DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *H. antrosom percarinatum*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
6.87	15 hrs. 20 min.	10.5-29.0	0.78	0.00740
6.84	14 " 45 "	15.5-30.5	0.96	0.00951
9.65	12 " 55 "	21.0-28.0	1.12	0.00898
10.38	15 " 35 "	22.0-30.5	1.18	0.00729
8.97	17 " 30 "	20.0-32.0	1.26	0.00802
8.69	16 " 15 "	24.5-30.0	1.32	0.00934
			Average	0.00842
4.34	26 hrs. 25 min.	5.5	0.12	0.00104
7.82	26 " 10 "	5.5	0.58	0.00283
9.17	23 " 25 "	5.5	0.62	0.00288
11.21	23 " 45 "	5.5	0.76	0.00285
8.69	26 " 15 "	5.5	0.82	0.00359
9.42	36 " 15 "	5.5	1.06	0.00310
			Average	0.00271

TABLE 34
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *H. trivolvis*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
18.62	15 hrs. 00 min.	10.5-28.0	4.35	0.01757
16.48	14 " 30 "	15.5-30.5	3.60	0.01506
17.28	12 " 42 "	21.0-28.0	3.45	0.01571
13.14	15 " 25 "	22.0-30.5	1.95	0.00961
11.21	17 " 20 "	20.0-32.0	2.40	0.01246
12.15	16 " 00 "	24.5-30.0	2.45	0.01260
20.92	16 " 10 "	16.0-31.5	3.60	0.01064
16.17	16 " 30 "	14.5-25.3	3.30	0.01236
			Average	0.01300
12.17	26 hrs. 10 min.	5.5	1.16	0.00364
21.32	26 " 20 "	5.5	1.52	0.00270
14.18	26 " 00 "	5.5	1.04	0.00282
10.29	23 " 30 "	5.5	0.76	0.00314
13.16	23 " 34 "	5.5	0.84	0.00270
12.17	36 " 00 "	5.5	1.16	0.00264
16.19	24 " 30 "	5.5	1.32	0.00332
			Average	0.00299

TABLE 35
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *L. stagnalis appressa*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption c.c. per gm. wt. per hr.
24.62	26 hrs. 00 min.	14.5-28.0	14.52	0.02268
33.09	19 " 00 "	15.5-30.5	12.54	0.01994
46.21	11 " 00 "	21.0-28.0	15.18	0.02986
18.16	10 " 30 "	22.0-30.5	6.48	0.03398
37.38	8 " 15 "	20.0-32.0	11.76	0.03812
36.81	8 " 00 "	24.5-30.0	12.24	0.04156
32.46	22 " 00 "	16.0-31.5	12.90	0.01806
34.17	30 " 00 "	14.5-25.3	31.20	0.03043
30.07	11 " 30 "	24.0-25.3	9.90	0.02862
19.92	9 " 00 "	23.0-29.0	5.88	0.03279
			Average	0.02960
34.16	25 hrs. 00 min.	5.5	6.60	0.00772
16.18	25 " 00 "	5.5	4.30	0.01063
12.43	26 " 00 "	5.5	3.60	0.01113
23.09	25 " 00 "	5.5	5.45	0.00944
26.72	23 " 30 "	5.5	6.55	0.01043
15.11	27 " 00 "	5.5	1.95	0.00477
14.36	23 " 00 "	5.5	2.10	0.00635
19.19	20 " 00 "	5.5	4.30	0.01120
15.84	18 " 30 "	5.5	1.40	0.00477
			Average	0.00849

TABLE 36
DISSOLVED OXYGEN CONSUMPTION OF SUBMERGED *L. megasoma*

Wt. in grams	Time submerged	Temperature in C.	Oxygen consumed in c.c. per l.	Average oxygen consumption in c.c. per gm. wt. per hr.
38.64	10 hrs. 30 min.	18.0-31.0	12.40	0.03056
37.19	10 " 35 "	20.0-31.0	13.05	0.03316
42.72	10 " 40 "	28.0-29.0	15.20	0.03334
32.85	10 " 45 "	27.0-28.0	11.65	0.03298
28.62	10 " 50 "	24.5-28.0	11.30	0.03645
29.18	10 hrs. 55 min.		Average	0.03329
27.49	11 " 00 "	5.5	6.05	0.01900
39.18	11 " 5 "	5.5	6.95	0.01685
40.07	11 " 10 "	5.5	6.70	0.01543
36.42	11 " 15 "	5.5	7.00	0.01563
			6.45	0.01574
			Average	0.01653

TABLE 37
OXYGEN CONSUMPTION OF GROUPED AND SEPARATED SNAILS

Species	Time submerged	Temp. in degrees C.	Wt. in gm.		Oxygen consump. in c.c. per l.		Avg. O ₂ consump. in c.c. per gm. wt. per hour	
			Grouped	Separated	Grouped	Separated	Grouped	Separated
<i>L. megasoma</i>	11 hrs.	25.5-28.8	14.3	13.8	5.40	4.82	0.0343	0.0317
<i>L. stagnalis appressa</i>	15 hrs.	22.2-27.8	13.7	13.2	4.82	4.08	0.0234	0.0206
<i>L. emarginata angulata</i>	21 hrs.	20.0-28.8	14.1	13.4	2.58	2.50	0.0086	0.0089
<i>H. trivolvis</i>	18.25 hrs.	21.0-30.0	14.6	14.4	3.74	3.91	0.0139	0.0148
<i>P. parkeri</i>	25 hrs.	20.0-28.8	12.3	13.8	3.67	3.80	0.0118	0.0110

